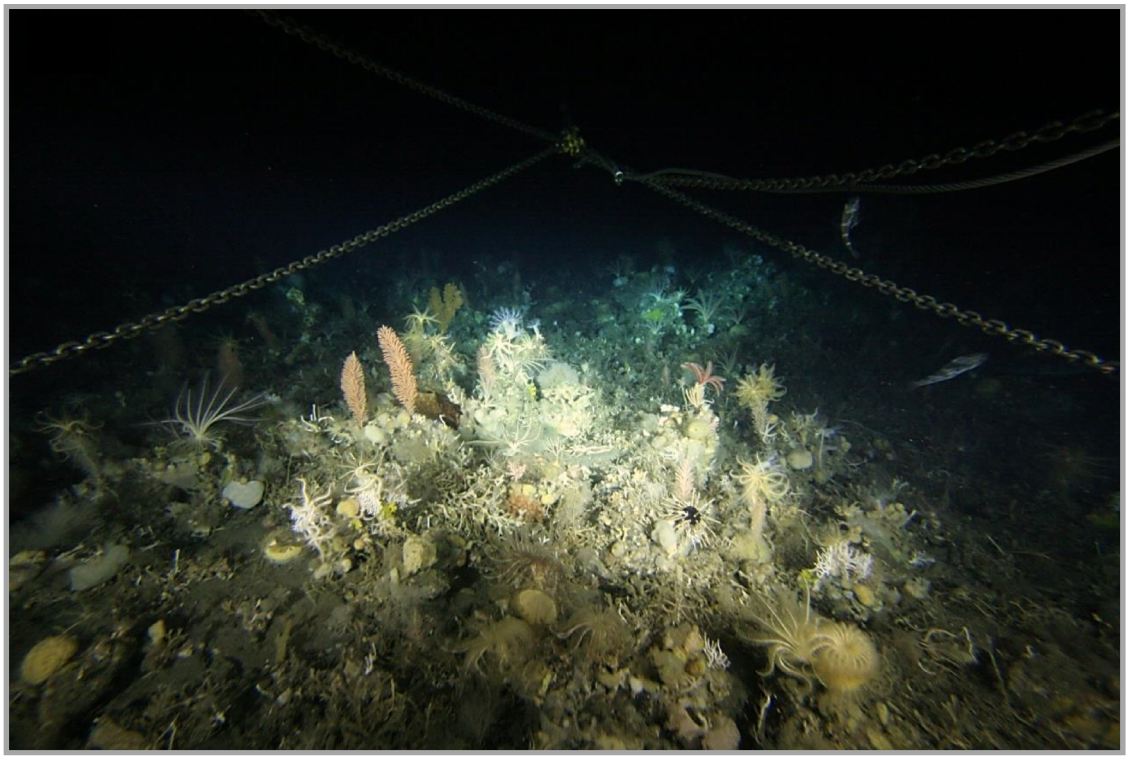
Describing and predicting the spatial distribution of benthic biodiversity in the sub-Antarctic and Antarctic



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Abstract

The global imperative to sustainably manage deep-sea bottom fisheries and mitigate impacts to benthic habitats is constrained by the limited existing biological data available to inform decision-making. Physical surrogacy, where benthic biodiversity is characterised based on its relationship with environmental parameters, was explored as a means of extrapolating the distribution and biomass of benthic species from sample sites to seascapes of the deep-sea. The evaluation of surrogates focused on those benthic species considered most susceptible to disturbance from bottom fishing gears including sponges and corals (termed 'vulnerable taxa') and data from the sub-Antarctic Heard and McDonalds Islands (HIMI) region. HIMI hosts an established bottom fishery with protection for biodiversity afforded through a large marine protected area (MPA). However whether the MPA meets CAR principles (comprehensive, adequate and representative) in the context of vulnerable taxa remains largely unknown due to a limited understanding of the HIMI benthic habitats.

To readdress the paucity of basic information and provide empirical data with which to develop predictive models, quantitative benthic samples were collected from 104 stations in depths of 200 to 1000 meters and analysed to document benthic biodiversity and community structure across HIMI. Data from HIMI were then used to develop surrogacy methods that were applied to other regions in the deep sea.

A total of 312 taxa were recorded in the deep-sea at HIMI. Diversity was dominated by sessile suspension-feeders, including numerous undescribed and possibly endemic taxa, and was similar to other sub-Antarctic islands but lower than rich areas on the continental shelves of Antarctica and Australia. Analyses of assemblage structure using taxa biomass records and the clustering method *Partitioning Around Medoids* revealed a clear zonation between HIMI's eastern and western banks, the central plateau, south-facing slopes and waters deeper than 500 m, which was driven mostly by changes in seafloor current speed, temperature and the concentration of particulate organic carbon. Disturbance from bottom fishing was not identified as an important proxy for biodiversity despite extensive trawling for more than 10 years, and instead suggests a strong link between benthos and environmental parameters, highlighting the vulnerability of these communities to changing environmental conditions. Similarly, the restricted distributions of many taxa and levels of endemicity in some groups highlight the uniqueness and vulnerability of the HIMI benthic habitat and importance for conservation. Nonetheless, it was acknowledged that the study failed to sample

the most heavily trawled areas at HIMI and that further taxonomic scrutiny (e.g. bryozoans are largely unsorted at this stage) might impact the study conclusions.

From empirical data at HIMI, ten vulnerable taxa were selected for which there were sufficient observations for model training (n >50). Four modelling approaches were contrasted to determine an appropriate method to model and predict vulnerable taxa across HIMI using physical surrogates: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT) and random forests (RF). For each method, two sequential models were constructed; one to predict the occurrence probability of each vulnerable taxa (termed 'occurrence model') and one to predict the biomass of that vulnerable taxa given their presence in an area (termed 'biomass model'). To contrast model performance, data were split into training and test datasets (cross-validation) and predictions evaluated using a series of performance indices relating to accuracy, calibration and bias between observed and predicted values. RF was identified as the preferred method to further explore and predict vulnerable taxa across HIMI due to consistent good performance (i.e. good accuracy, good calibration and low bias between observed and predicted values) and hence predictions were made using this approach. The predictions of occurrence and biomass of vulnerable taxa across the HIMI seascape indicated a higher frequency and biomass in shallow depths (<500 m), and on complex seascape features (e.g. HIMI's banks and craggy slopes), compared with the deeper areas of the plateau. Analysis of predictions using the conservation planning software *Zonation* highlighted HIMI's banks and numerous areas across the central plateau and continental slope as priority areas for conservation, many of which are currently protected by the MPA.

To test the broader applicability of the RF framework, models of vulnerable taxa were subsequently constructed for the continental shelf of East Antarctica (30°E – 150°E) where the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is considering the adoption of a Representative System of MPAs (RSMPA). Like HIMI, the benthos here are poorly described and marine conservation planning may benefit from model estimates to assist decision making. Benthic samples from the region and collocated environmental variables (including sea ice properties) were used to parameterise RF models for eight vulnerable taxa that were classified using the same principles as for HIMI. Both the occurrence and biomass models returned high accuracy according to the indices used, suggesting a high level of confidence in predictions across East Antarctica, and highlighting the transferability of the RF framework to other seascapes. Model estimates revealed a number of hotspots, namely the Prydz Bay region, but also Gunnerus Ridge, west of both Enderby Land and Casey Station and patches between Adelie Land and George V Land, the majority of which are encompassed within the proposed RSMPA.

Importantly the model estimates presented in this study suggest that CAR principles have been achieved for vulnerable benthos in the HIMI and (proposed) East Antarctic MPAs. In developing these MPAs, the distribution and hence representativeness of protection for benthic habitats and their biota within the MPA was inferred largely from physical variables as the empirical data required to characterise these habitats were sparse or not available at the time. My predictive modeling results that do incorporate empirical data and have produced similar recommendations for biodiversity conservation at HIMI and in East Antarctica suggest that the use of physical surrogates were an adequate tool for marine planning in the absence of biological data in these systems. More broadly, the results suggest that management or mitigation measures for benthos based on physical parameters may provide adequate precautionary management in other marine ecosystems where the empirical data necessary to evaluate the benthic habitat are lacking.

The accuracy of predictions and transferability of the RF framework means that methods developed here might be readily applied to other seascapes where decision-making may benefit from predictions. Sample size, model extent and data resolution were all potential sources of uncertainty which would best be addressed through targeted field sampling and surveys. However given the immediacy of the issue of managing bottom fishing to prevent significant adverse interactions with vulnerable ecosystems, and the practical difficulties associated with obtaining empirical data, surrogate-based management is the only practical means to make reasoned decisions about high seas resource management and for the establishment of a CAR system of MPAs throughout the Southern Ocean.

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Introduction

Loss of marine biodiversity and damage to ecosystems through anthropogenic disturbances is of global concern and well documented (e.g. Pauly *et al.* 2005, Kaiser *et al.* 2006, Bindoff *et al.* 2007, Halpern *et al.* 2008, Jackson 2008). In response, the international community is supporting increased implementation of marine protected areas (MPAs) (Lubchenco *et al.* 2003). However the biological information necessary to inform conservation and management decisions is often lacking in the marine environment (Hendriks *et al.* 2006). This is especially true for benthic ecosystems in the deep-sea despite increasing concerns over impacts from anthropogenic activities.

A practical solution to developing conservation strategies for the deep-sea benthos (organisms living in or on the seafloor) is to predict patterns of biodiversity based on physical surrogates (e.g. Zacharias & Roff 2000, Oppel & Huettmann 2007, Wei *et al.* 2010). The use of physical properties as predictors of biota has the advantage that abiotic parameters like water depth are readily available across large spatial scales and can be evaluated in a timely and inexpensive manner using advanced statistical methods and modern-day computational power. In an era of limited conservation resources (e.g. time, money) (Rodrigues & Brooks 2007), surrogacy models are increasingly being explored as a complimentary tool to assist with spatial management of marine biodiversity (e.g. Hockey & Branch 1997, Guisan & Thuiller 2005, Elith *et al.* 2006, Guisan *et al.* 2006b, Oppel & Huettmann 2007), and are contributing increasingly to the selection and ongoing monitoring of MPAs (e.g. Hockey & Branch 1997, Pickrill & Todd 2003, Harris 2007).

Here I explore the use of physical surrogacy models for deep-sea benthic biodiversity, specifically that in sub-Antarctic Heard and McDonalds Islands (HIMI) region and East Antarctica, areas where an assessment of the benthic habitat is necessary to ensure comprehensive, adequate and representative MPAs.

Deep-sea bottom trawl fisheries and their impacts on biodiversity

The deep-sea is one of the last major frontiers on the planet. The ocean floor beyond 200 metres, where the deep-sea begins, covers more than 50 percent of the entire surface of the Earth and yet it is suggested that more is known about the moon than the deepest parts of the ocean (Flannery 2007). Though only a small fraction of these ecosystems has been studied, research has revealed remarkably high levels of biodiversity and endemism, comparable to that of tropical rainforests or shallow-water coral reefs (Gianni 2004). As such, the deep ocean is increasingly being recognised as a major global reservoir for marine biodiversity and a host for many complex and diverse habitats.

As with all ecosystems, the deep-sea is under increasing pressure from anthropogenic activities. While oil and gas exploration, seabed mining and human-induced climate change can ultimately have a negative effect on deep-sea species, by far the most widespread activity affecting the biodiversity of the deep-sea today is bottom trawl fishing (Gianni 2004).

Ever since bottom trawling began there have been concerns over its impact on deep-sea habitats and, in particular, on corals, sponges and other "sessile" species which form the basic structure of biologically diverse deep-sea benthic ecosystems (De Groot 1984, Collie *et al.* 1997, Hiefetz 2002, Puniwai 2002, Gianni 2004, Tissot *et al.* 2004b, Auster 2005b). Deep-sea bottom-trawling involves towing a net directly along the sea floor for up to several hours at a time during which the net and associated gear (trawl "doors", chains, cables, chaffing mat etc.) are in almost continuous contact with the seafloor (Gianni 2004). As such, invertebrate species living on or attached to the seabed are at risk to physical damage or mortality upon interaction with bottom fishing gear. This can most easily be understood by considering the example of a vulnerable deep-sea habitat like that in Fig. 1 which would inevitably be damaged or destroyed by bottom trawl gear.

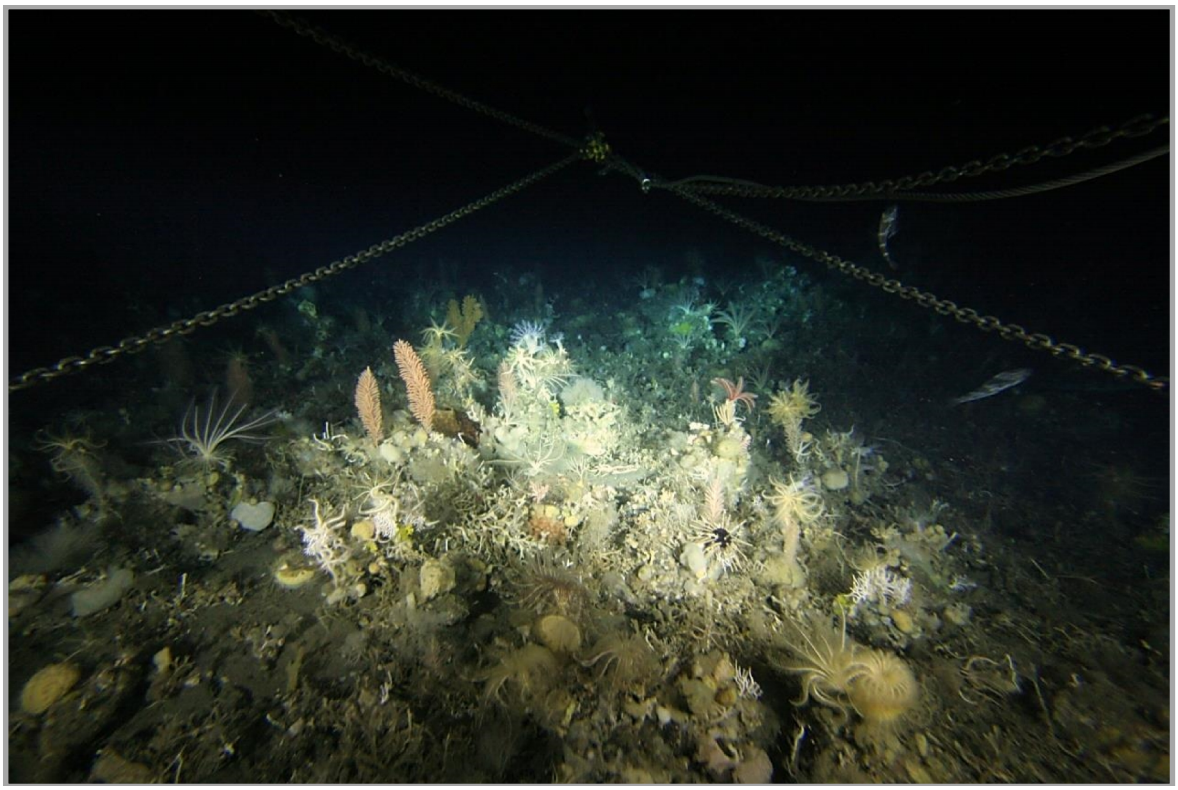

Fig. 1 An example of vulnerable deep-sea benthic habitat structured by sessile suspension-feeding taxa including numerous sponges, deep-sea corals, tube-worms and bryozoan matrices. Living within these habitat-forming organisms is a diverse array of molluscs, crustaceans, echinoderms and benthic fish. The habitat pictured, which was photographed on the continental shelf of East Antarctica at approximately 520 m depth, may be considered a vulnerable deep-sea ecosystem.

Numerous studies have shown bottom trawl fishing to be highly destructive to the biodiversity associated with deep-sea ecosystems (e.g. Collie *et al.* 1997, Jennings *et al.* 1999a, Collie *et al.* 2000, Koslow *et al.* 2001, Hiddink *et al.* 2006). Observed changes range from destruction of habitat structure (Koslow *et al.* 2001) through the local extinction of species (Hiddink *et al.* 2006) to wholesale shifts in the functioning of entire ecosystems (Kaiser *et al.* 2000, Jennings *et al.* 2001). For example Koslow *et al.* (2001) found that benthic biomass was 106% greater on un-trawled seamounts south of Tasmania compared with heavily fished seamounts and there were 46% more species recorded on un-trawled compared to trawled seamounts. Similarly Fossa *et al.* (2002) estimated that 30-50% of deep water *Lophelia pertusa* (coral) reefs off Norway had been impacted or destroyed by bottom fishing gear and Collie *et al.* (1997) observed a shift in the dominant species from large, sessile suspension-feeders to smaller opportunists and scavengers in the north-west Atlantic. Overall, a reduction in physical and biological habitat heterogeneity are common outcomes of bottom trawling (Clark & Rowden 2009).

Long term impacts of bottom fishing are more difficult to discern but recovery from disturbance is likely to be prolonged and is not guaranteed. In the deep ocean factors such as low levels of energy input and an infrequent natural regime of disturbance that may occur over very long time scales has led to the evolution of life history strategies where organisms may grow slowly, live for decades or centuries, and have low dispersal capabilities (Martin-Smith 2009b, a). For example deep-sea corals have been recorded as old as 4,550 years on the continental slope west of Ireland (Hall-Spencer *et al.* 2002) and 8,500 years on Sula Ridge off Norway (Freiwald *et al.* 2002), with suggestions that many of the deep-sea coral reefs seen today probably date back at least 10,000 years (Rogers 1999). Estimates of time required to recover following disturbance range from 10-45 years for bryozoans in colder habitats (Barnes & Conlan 2007), 130-200 years for gorgonian corals in the Southern Ocean (Martin-Smith 2009b, a) and 340 years for sponge communities in the Weddell Sea (Gutt & Starmans 2001). The extremely high maximum ages for some deep-sea corals would suggest that recovery times after disturbance may be considerably greater than those examples cited above. Bottom fishing possesses a significant risk to these long-established populations, including the possibility of species extinctions, highlighting the need for conservation of vulnerable deep-sea ecosystems to avoid potentially irreversible impacts.

Conservation and management of deep-sea benthic biodiversity and current challenges for decision-makers

The requirement for governments to implement strategies for the conservation and sustainable use of biological diversity has existed for decades. These requirements are warranted under the *Convention*

on Biological Diversity (CBD) incepted in 1992, and have been reinforced at three Earth Summits subsequently (Rio 1992; Johannesburg 2002; Rio 2012). More recently the United Nations (UN) General Assembly in 2006, recognising the vulnerability of deep-sea biodiversity, called upon all States and regional fisheries management organisations and arrangements (RFMO/As) to "*protect vulnerable marine ecosystems…from destructive fishing practices*" or cease bottom fishing activities in areas where vulnerable marine ecosystems (VMEs) such as cold-water coral reefs or sponge fields are known or likely to occur (61/105).

Protection of marine biodiversity would typically be achieved through a fisheries closed-area or designation of an MPA. Maintaining areas that are closed to fishing offers the most straightforward and risk-averse strategy to mitigating impacts. Closed-areas were essential to the protection of a deep-water *Oculina varicosa* coral reef systems off eastern Florida (Reed *et al.* 2007) and would be best suited to areas where VMEs are known to occur. Alternatively, an MPA may be proposed which is essentially a space in the ocean where human activities may still occur but are more strictly regulated than the surrounding waters. This strategy has been used by the Government of South Georgia and the South Sandwich Islands who created a large MPA designed to ensure the protection and conservation of the region's rich and diverse marine life, whilst allowing sustainable and carefully regulated fisheries (Trathan *et al.* 2014).

To meet the objectives of the UN General Assembly, and protect vulnerable deep-sea ecosystems, identification of VMEs or areas where concentrations of vulnerable taxa are known or likely to occur, is necessary. Ideally VMEs would be identified based on comprehensive empirical data. Unfortunately, data on the deep-sea benthos is scarce and further sampling to address this deficit would be time consuming and expensive (Balmford *et al.* 2004). As such the empirical data warranted to address conservation targets are unlikely to become available in the near future. This situation has led to the development of complimentary planning tools which make best use of limited conservation resources. One such tool which is receiving increasing attention is surrogacy modelling.

Physical surrogates for vulnerable deep-sea ecosystems

Surrogacy models use observed relationships between biota and their environment to make predictions at large spatial scales (100s of kms). Where relationships are observed (i.e. surrogate relationship, also referred to as "proxies"), an assumption is made that the presence of an organism will be similar in areas where physical properties are also similar. By using surrogate relationships and synoptic layers of environmental data (e.g. depth), predictions can be made, providing a means to extrapolate distributions at relevant spatial scales (i.e. across fisheries).

Terrestrial studies have long established the usefulness of environmental factors as estimator surrogates of biodiversity (Dalleau *et al.* 2010). Results have been mixed, but are generally valuable to guide the decision making processes for management and conservation of species or habitats across spatial-scales larger than can be readily sampled using traditional techniques (e.g. Howard *et al.* 1998, Andelman & Fagan 2000, Ferrier 2002, Lund & Rahbek 2002, Sarkar *et al.* 2004, Altmoos & Henle 2007, Rodrigues & Brooks 2007).

The utility of physical surrogates for benthic marine biodiversity is less well known. The study of benthic habitats and their distributions has often focused on the association between biodiversity and components of the physical habitat (Hixon *et al.* 1991a, Stein 1992, Auster *et al.* 1995, Yoklavich *et al.* 2000, Nasby-Lucas *et al.* 2002) with clear and well documented relationships against parameters like depth, current speed and substratum type (e.g. Snelgrove & Butman 1994, Post 2006, Ward *et al.* 2006b, Williams *et al.* 2010, Post *et al.* 2011). Only recently however, with the advent of powerful statistical tools and the processor power to run models based on large datasets (e.g. Generalised Linear Mixed Models, Random Forest, Boosted Regression Trees, etc), and the increasing availability and spatial resolution of marine physical data worldwide (i.e. remote sensed data), have scientists been able to better characterise these relationships to establish surrogates of marine biota and robust predictive models (McArthur *et al.* 2009). Physical surrogates have since been used to predict the spatial distribution of benthic species, taxonomic groups, or communities as a function of environmental gradients (Guisan & Thuiller 2005, Elith *et al.* 2006, Guisan *et al.* 2006b, Oppel & Huettmann 2007), and are contributing increasingly to the selection and ongoing monitoring of MPAs throughout the world (e.g. America (Greene *et al.* 1995), Australia (Harris 2007), Canada (Pickrill & Todd 2003) and South Africa (Hockey & Branch 1997)).

Use of physical surrogates to assess seascapes (i.e. the marine domain across which an assessment is performed) has the advantage that many parameters such as water depth or bottom water temperature can be measured relatively easily and consistently across wide areas (Post 2008), facilitated by recent advances in satellite remote sensing and associated online data archives such as the CSIRO Atlas of Regional Seas (Ridgway *et al.* 2002) or NASA's OceanColor Web Site (Feldman & McClain 2010). Furthermore, advances in oceanographic modelling like the CAISOM Ocean Model (Galton-Fenzi *et al.* 2012) means that our understanding of ocean processes, particularly at the seafloor, is greater than ever. For example Wei *et al.* (2010) capitalised on recent advances in marine physical data and benthic sample data collated by the Census of Marine Life (CoML) to predict global seafloor biomass and abundance for major size groups (i.e. bacteria, meiofauna, macrofauna and megafauna) across Earth's oceans. Maps of estimated faunal composition like those produced by Wei *et al.*

(2010) provide a valuable tool with which to assess seascapes and are particularly important to guide management decisions where minimal biological information is available.

As with all predictive models there are uncertainties which must be considered when adopting such an approach. In the marine environment this uncertainty can be introduced from a number of sources. First is the quantity of available biological data. Numerous authors have shown that sample size and the number of presence records greatly influences model performance and, not surprisingly, suggest that model accuracy would benefit from further targeted sampling (McPherson *et al.* 2004, Reese *et al.* 2005, Guisan *et al.* 2006a, Meynard & Quinn 2007). Second is the underlying environmental data. Many surrogacy studies included readily available sea-surface parameters like Chlorophyll-*a* as proxies for benthic fauna (e.g. Oppel & Huettmann 2007, Constable *et al.* 2010, Wei *et al.* 2010) despite a poor understanding of the link between sea surface parameters and productivity at the seafloor (Wei *et al.* 2010). Samples are often collected across several seasons or years and yet temporal variability is also often ignored (e.g. Pearson & Cassola 1992, Erdmann & Caldwell 1997, Olsgard & Somerfield 2000, Wei *et al.* 2010). In such instances, it is inadvertently assumed that bio-physical relationships remain consistent through time, when in fact seasonal patterns in biota and physical variables may play an important role in structuring benthic ecosystems. Uncertainty is also introduced by the associated level of taxonomy. Although several studies have shown that identification at coarse taxonomic levels (e.g. order level; Wlodarska-Kowalczuk & Kedra 2007), and even major size classes (e.g. megafauna; Wei *et al.* 2010), showed sufficient relationships to detect community response to environmental gradients, at the species level organisms will react to their habitat (Bertrand *et al.* 2006), and hence analyses and prediction at at finer taxonomic resolution is likely to have the greatest power to detect relationships between biotic and abiotic variables (McArthur *et al.* 2009).

The above highlights the importance of considering the nature of the underlying data (both biotic and abiotic) prior to pursuits in surrogacy modelling. Nonetheless in the data poor deep-sea surrogate-based management of biodiversity is the only practical means to make reasoned decisions about high seas resource management (McArthur *et al.* 2009). A vast area of deep-sea which is particularly data poor, and would benefit from complimentary conservation planning tools such as surrogacy modelling, is the deep Southern Ocean.

Application of physical surrogacy to the deep Southern Ocean

Benthic ecosystems in the deep Southern Ocean have been shown to harbour significant levels of biodiversity yet remain some of the most poorly understood on the planet (Clarke & Johnstone 2003,

Gutt *et al.* 2004, Brandt *et al.* 2007) despite established bottom fisheries in Antarctic and sub-Antarctic waters (bottom trawl, long-lines, pots/traps and bottom-set). These bottom fisheries are likely to represent the most immediate disturbance acting on the benthos of the deep Southern Ocean today (Kock 2007). The habitats targeted by these fisheries are considered to experience low levels of natural physical disturbance, typically being at depths beyond the influence of surface processes such as storms or iceberg scour. Consequently, communities and their biota are thought to have low resistance to physical disturbance and a poor ability to recover following impact (White 1984). Moreover, the presumed slow growth rate, relatively low abundances, patchiness or isolation and restricted larval dispersal of many Antarctic and sub-Antarctic benthic species highlight the particular vulnerability of the Southern Ocean communities (Martin-Smith 2009b).

To meet the requirements of the UN General Assembly Resolution 61/105 (i.e. protect VMEs), the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the body responsible for managing fishing activities in the Southern Ocean, has committed to avoiding significant adverse impacts on VMEs and is actively involved in developing management strategies to minimise impacts (CCAMLR 2008). To assist with this process, surrogacy models developed on the information (both empirical and theoretical) that we currently have available should be considered. Developing model predictions was identified as a priority for the Southern Ocean at the Workshop on Vulnerable Marine Ecosystems (WS-VME; La Jolla, USA, August 2009) convened to assist CCAMLR meet is conservation objectives regarding VMEs (WS-VME 2009). At WS-VME it was noted that in some locations, biological data already assembled may be adequate to evaluate the use of physical surrogates for VMEs in the Southern Ocean, and it was urged that where these data exist, analyses be pursued (WS-VME 2009). One such Southern Ocean ecosystem is the region of the Heard and McDonald Islands (HIMI) (Fig. 2).

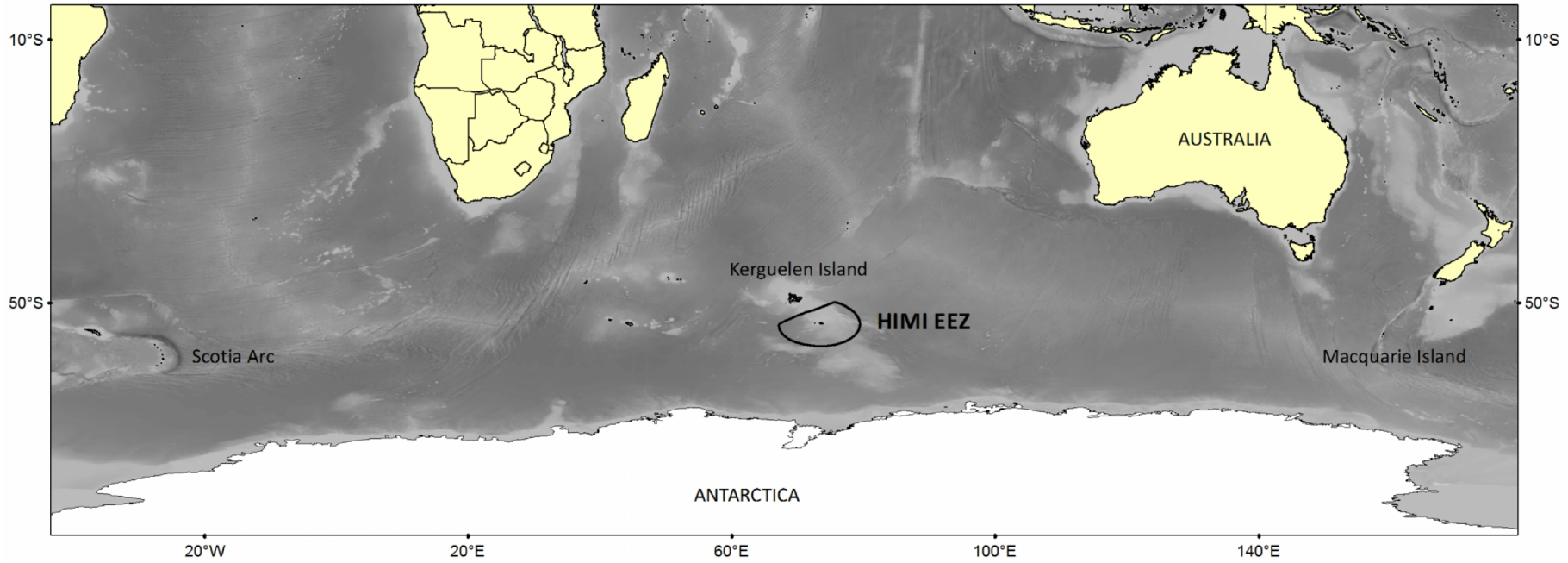

Fig. 2 Map of the Southern Ocean region showing the location of Heard Island and McDonald Islands (HIMI) Australian Exclusive Economic Zone (EEZ) in relation to Australia, Antarctica and similar sub-Antarctic islands like Macquarie Island.

A case study for Heard Island and McDonald Islands (HIMI)

HIMI forms part of Australia's sub-Antarctic region and hosts an established bottom fishery, yet the benthic habitat remains poorly described and understood. It is an area where spatial protection of biodiversity has been identified as a priority issue (Commonwealth-of-Australia 1998, IMCRA-Technical-Group 1998), and one where precautionary conservation measures are in place (Welsford *et al.* 2013) yet require validation to ensure representative or vulnerable habitats are protected from the cumulative impact of the HIMI fishery. It also lies in an area of Australian national jurisdiction where there are further obligations under *Environmental Protection and Biodiversity Conservation Act 1999* (EPBC Act) and *Fisheries Management Act* 1991 (FM Act) to ensure activities are sustainable and biodiversity is conserved (Welsford *et al.* 2013).

Whilst HIMI is data-poor compared to some less remote and shallower regions, by Southern Ocean standards it is well researched. In this regard, HIMI provides a unique opportunity to establish surrogacy methods that may be applied to other regions in the deep-sea.

The marine environment at HIMI

The HIMI region is situated in the Indian Ocean sector of the Southern Ocean, about 4100 km southwest from the coast of Western Australia, a similar distance southeast of South Africa and 1700 km north of Antarctica (DEH 2002) (Fig. 2). HIMI forms Australia's most remote sovereign territory and one of two Australian Exclusive Economic Zones (EEZ) distant from the continental EEZ in temperate and sub-Antarctic waters.

The emergent part of Heard Island is dominated by Laurens Peninsula and Big Ben; a conical volcano whose apex, Mawson Peak, is 2 745 m high and displays minor sporadic activity (Quilty *et al.* 1983). The McDonald Islands consist of three separate islands: Meyer Rock, Flat Island and McDonald Island; the latter being the largest with a maximum elevation of 186 m (Quilty *et al.* 1983).

The islands (Heard and McDonald) arise from the northern half of the Kerguelen Plateau, which is one of the largest oceanic ridges in the world and the largest in the Southern Ocean. The plateau extends 2100 km in a north-westerly direction from continental Antarctica into the Indian Ocean, roughly between 45ºS to 63ºS and 65ºE to 83ºE. It is about 500 km across and rises 3 to 4 km above the surrounding ocean floor to within a kilometre of the sea surface (Harris *et al.* 1998).

The region of the Kerguelen Plateau has been divided into five distinct geological domains: northern, central and southern portions, Elan Bank and the Labuan Basin (ODP 1998). The HIMI EEZ

encompasses the central portion, and includes a diversity of physical habitats including mesa-like banks, plateau and intra-plateau features (e.g. mounds) and steep marginal slopes traversed by deep crevices and canyons (Fig. 3). The characteristics of marine habitats across HIMI, termed *physical units* (sensu Meyer *et al.* 2000), are summarised in Table 1.

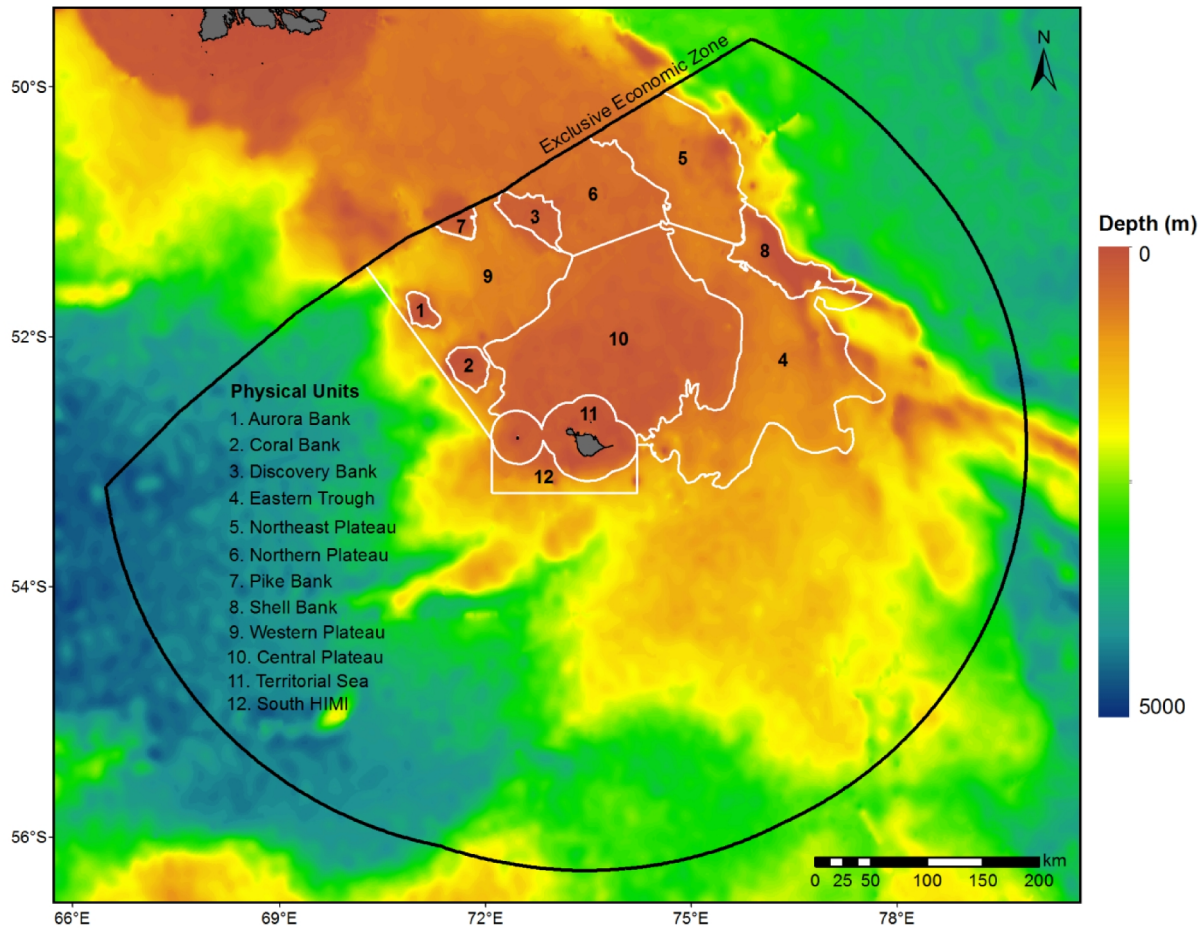

Fig. 3 Physical units throughout the HIMI EEZ. These units were outlined and described by Meyer *et al.* (2000) in their review of the HIMI marine environment.

Table 1 Physical units throughout the HIMI EEZ described with reference to Meyer *et al.* (2000) and current state of knowledge. Depth range (m) was derived from the Kerguelen Digital Elevation Model (KDEM) of Beaman and O'Brien (2011). Geomorphology was interpreted from the Kerg_dem and substrate descriptions from reports of the Ocean Drilling Project (ODP 1998). Oceanographic data from van Wijk *et al.* (2010) were used to infer local productivity and currents. Substratum and oceanography are discussed in detail in later sections.

Physical unit	Geomorphology	Depth range (m)	Substratum	Oceanography
Coral Bank	Relatively flat, mesa-like bank rising steeply from deep water.	300 - 500	Rugged top with pinnacles, boulders and a covering of sand.	Locally highly productive in relatively warm, nutrient-rich waters of the Antarctic Circumpolar Current (ACC).
Aurora Bank	Large, relatively flat, mesa-like bank rising steeply from deep water.	300 - 500	Top is rugged with pinnacles, boulders and a covering of sand.	Locally highly productive in relatively warm, nutrient-rich waters as it is one of two banks that first intercepts the ACC.
Discovery Bank	Whale-backed bank rising from the Northern Plateau.	300 - 400	Reasonably flat with basaltic sand, but can be pebbly and craggy in places.	Influenced by relatively warm water of the ACC.
Pike Bank	Flat topped bank, eastern slopes are relatively steep.	300 - 500	Flat on top but pebbly and gnarly on the slopes.	Influenced by the ACC and the northern passage of the Polar Front.
Shell Bank	Isolated mesa-like bank.	180 - 350	Flat, even top with steep craggy slopes and craggy rim. White sand and thick shell grit deposit unique to area.	Relatively cool water around the bank and an eddy of productive water influences it. Cool water also moves up through the trough to the west.
Central Plateau	Broad, flat and even substratum with east and west margins generally steep and undulating to craggy slopes.	200 - 500	Mostly smooth, medium-grain black basaltic sand and grey silt.	Area is influenced by relatively warm water of the ACC in the west and northwest of this unit, some effect of cooler water from Eastern Trough.
Northern Plateau	Relatively narrow region of the main plateau with uneven topography	500 (avg)	A hard substratum of basaltic cobbles, small pinnacles, black sand and grey silt.	Cooler water from the Eastern Trough and the relatively warm water of the ACC in the west and central part of this unit influence the area.
Northeast Plateau	Sloping into deeper water in the east.	500 - 700	Hard substratum with cobbles, yellow sand and grey silt.	Area is influenced by cooler water from the trough and is south of the Northern Polar Front.
Eastern Trough	Wide in the southern part.	750 (avg)	Fine grey sand and silt.	Cooler water from either the eddy in the lee of the plateau and/or of Antarctic origin.
Western Trough	Topographically similar to the Eastern Trough but it is deeper and more open to the influence of the ACC.	500 - >1500		Experiences the warmest waters, as this is the first location where the ACC encounters the plateau around HIMI.
Near-shore to HIMI including the Territorial Sea	Continental shelf seafloor. Increasing depths from nearshore HIMI. Steep sloping southern margin to >1000 m depth.	Generally 0 - 300, increasing rapidly to >1000 in the South	Mostly smooth with medium-grain black basaltic sand. Basaltic cobbles and boulders common in the nearshore area.	Substratum in this area is more disturbed by wave action than other areas. This occurs mostly in water shallower than 200 m, particularly in N, NE and E.
South of HIMI	Local unit is a relatively unknown deep-water area to the south of the units described above.	>1000	Siliceous diatom mud or ooze with some areas revealing quantities of calcareous sediments and foraminifera.	Generally experiences ACC.

Bottom fishing, conservation strategies and benthic research at HIMI

Since April 1997 an Australian bottom fishery targeting Patagonian toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*) has been in operation in the HIMI EEZ administered by the Australian Fisheries Management Authority (AFMA). The fishery operates in waters deeper than 500 m and includes bottom trawling, long-lining and experimental potting.

In recognition of the potential threat of bottom fishing on HIMI's biodiversity and obligations under the *Convention on Biological Diversity,* to which Australian is a signatory*,* a substantial MPA was established within the HIMI EEZ in October 2002 (AAD 2005). The HIMI MPA (also known as the HIMI Marine Reserve) is a Commonwealth Reserve, declared under section 344 of the EPBC Act, and is listed as an IUCN Category 1a Strict Nature Reserve. It includes the World Heritage listed islands and territorial sea, plus an additional marine area extending in parts to the 200 nautical mile EEZ boundary (Fig. 4). The declaration of a Conservation Zone under the EPBC Act was also initiated in October 2002 for identified MPA candidate areas to provide interim protection from threat of disturbance or damage (see Fig. 4). The management objectives for the MPA are described in the *Heard Island and McDonald Islands Marine Reserve Management Plan* (AAD 2005).

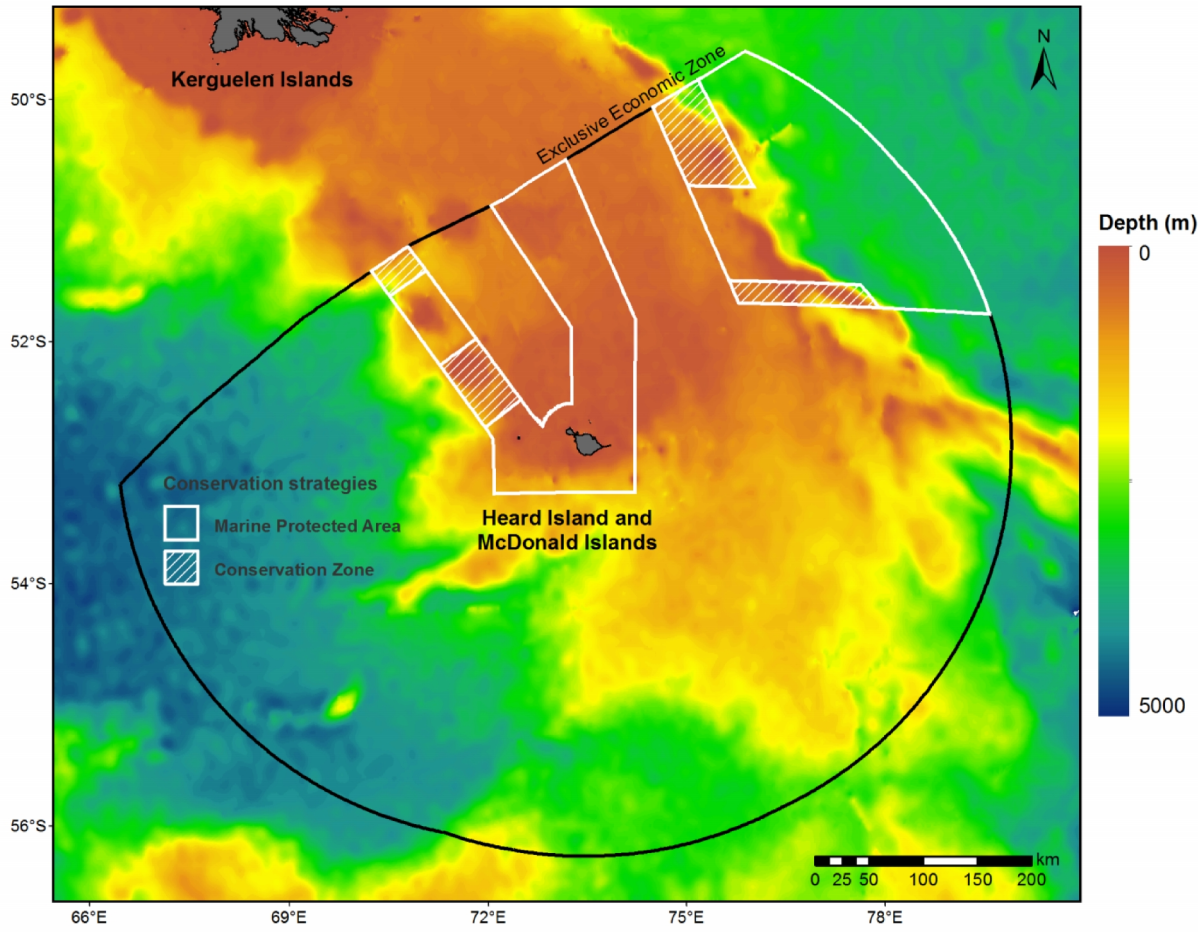

Fig. 4 Delineation of the HIMI marine protected area and conservation zones declared under the *Environmental Protection and Biodiversity Conservation Act 1999* in October 2002.

The MPA, including the conservation zones, was located with the goal of preserving representative marine conservation values of the HIMI region and was designed based on all scientific data available at the time, including data on biota and geophysical features of the area (Meyer *et al.* 2000, Welsford *et al.* 2011). However, a paucity of data on the benthos was noted and at the time of inception protection for benthic biodiversity in the HIMI MPA was largely precautionary. In particular for the conservation zones there was insufficient information available regarding their commercial fishing potential and conservation value to be included within the MPA boundaries and a further assessment of these areas was determined necessary before consensus could be achieved on their future status (DEH 2002).

Since the late 1800s more than 35 expeditions have surveyed the Kerguelen Plateau, yet only 7 of these have collected benthos from HIMI and predominantly from within the territorial sea (Meyer *et al.* 2000, Hureau 2009). Prior to 2002 HIMI-wide data were limited to samples collected incidentally from demersal fish surveys by the Australian Antarctic Division (AAD) (Williams & de la Mare 1995) and from by-catch from commercial trawlers since the commencement of the HIMI fishery.

These incidental qualitative samples were mostly identified to morphotype (i.e. representative of species), but provide good spatial coverage, at least in regards to the larger epibenthic fauna, as many smaller and fragile fauna (e.g. bryozoans, polychaetes etc) are likely to be underrepresented due to the behaviour and mesh-diameter of the fish-sampling equipment.

Meyer *et al.* (2000) provided a comprehensive synthesis of these data with reference to HIMIs physical units (see Table 1 and Fig. 3) which later formed the basis for benthic protection within the MPA design. They provided evidence of a diverse and distinctive array of benthic habitats across HIMI, supporting a range of slow growing and vulnerable benthos. However, despite evidence of change in species-assemblage composition across HIMI, the conclusions were largely speculative due to the sparse nature of the data. Hence in the MPA planning process it was highlighted that further assessment of the benthic habitat was necessary, in particularly for the conservation zones so that consensus might be achieved on their conservation value (DEH 2002). Extensive sampling of the benthic habitat of HIMI was subsequently undertaken in 2003, 2007 and 2008 in conjunction with the AAD's HIMI marine research program and studies into the potential impacts of bottom fishing practices on benthic habitats in Australia's high seas EEZ (Welsford *et al.* 2014a). More than 100 quantitative samples of the benthos have now been collected from numerous locations across the region, contributing to one of the largest datasets in the Southern Ocean. This data has since been used to identify important populations throughout the conservation zone and to evaluate and refine the MPA boundaries (Fig. 5). However, assessing conservation and management strategies for benthic habitats across HIMI requires an understanding of the distribution of fauna and assemblages at the scale of the fishery, including areas where fishing occurs but samples have not been collected. Research to determine the principle factors influencing the distribution of vulnerable taxa and ecosystems across HIMI, and to develop models to predict distributions, is therefore a priority to ensure conservation objectives of the MPA are achieved.

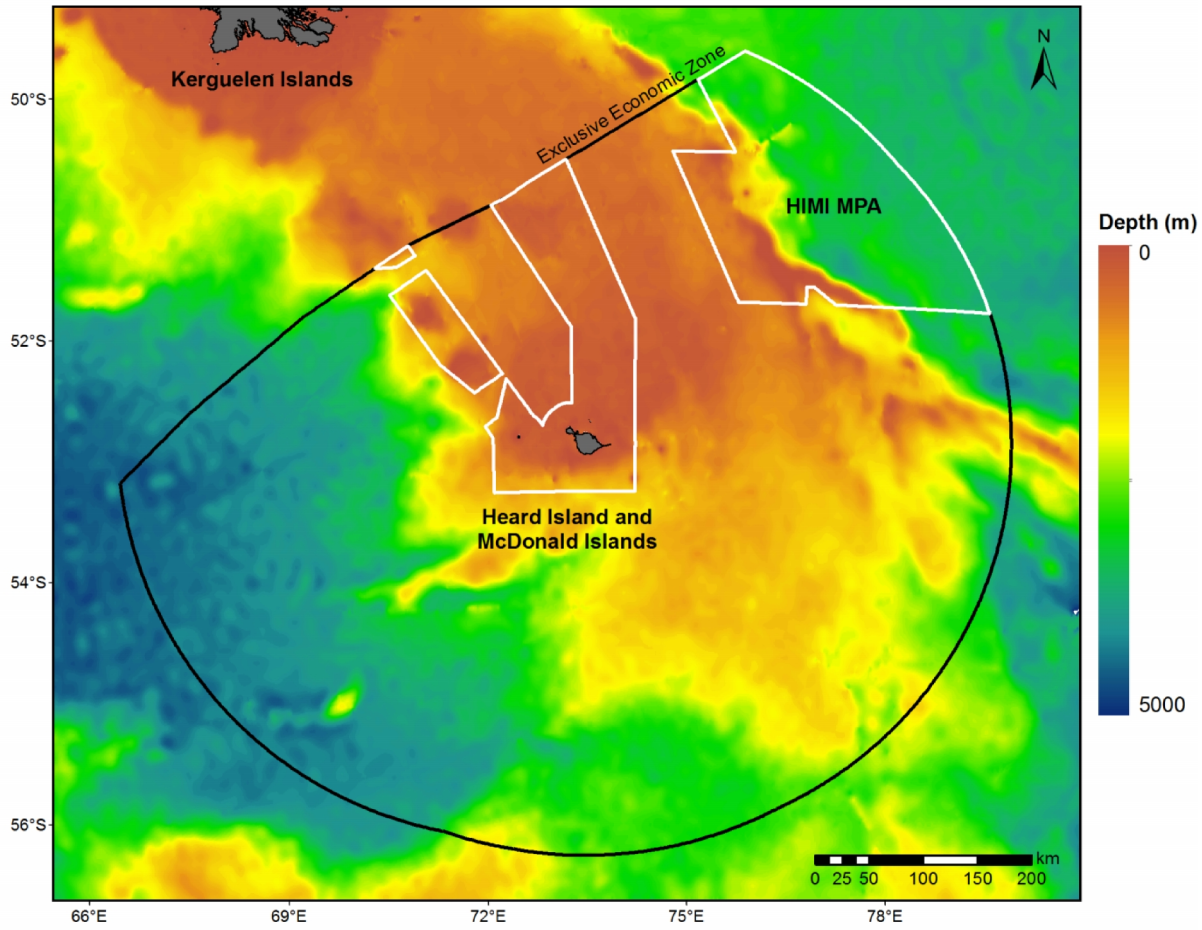

Fig. 5 The revised HIMI MPA (white boundary) which came into force in March 2014. The HIMI MPA now possesses an area of 71,200 square kilometres and includes further waters identified as of high conservation value. The HIMI MPA is Australia's largest IUCN 1a Strict Nature Reserve.

Research objectives

The overall objective of this study was to use quantitative data from the HIMI benthic habitat to develop a model framework to predict the spatial distribution and biomass of vulnerable taxa over large spatial scales (100s of kms). For the purpose of this study, 'vulnerable taxa' are those benthic species considered most vulnerable to damage or mortality from bottom-fishing gears (i.e. corals and sponges). Predictions of the spatial distribution and biomass of vulnerable taxa can then be used to evaluate current or future management strategies to facilitate better protection of benthic biodiversity in the deep Southern Ocean.

This thesis comprises four data chapters written as a series of standalone papers, each addressing specific objectives. A summary of the specific objectives of each chapter is outlined below.

Chapter 1 Natural and anthropogenic drivers of the structure and dynamics of sub-Antarctic benthic assemblages

Here I provide an assessment of the HIMI seascape, including benthic biodiversity and the relationship between benthos, environment and the potential vulnerability to bottom trawl fishing. This assessment provides baseline information with which to evaluate patterns in the distribution and biomass of vulnerable taxa and the effectiveness of existing management regimes to protect biodiversity and minimise impacts from bottom trawling.

Chapter 2 A comparison of four models for estimating patterns of vulnerable taxa across the Heard Island and McDonald Islands region

In this chapter I compare four alternate modelling approaches to determine the most appropriate method to model and predict vulnerable taxa across HIMI. The following questions were addressed:

(1) Is there a statistical technique that has a consistently higher predictive ability than others? and

(2) Is there a statistical technique that is more suited to exploring benthic datasets like those collected at HIMI with few observations and frequent non-detections?

Chapter 3 Improving protection of benthic biodiversity in the deep Southern Ocean using predictions of occurrence and biomass

Here I model and predict the distribution and abundance of vulnerable taxa across the HIMI. These predictions are used to identify high priority conservation areas and to evaluate the effectiveness of the HIMI MPA in protecting vulnerable marine benthos.

Chapter 4 Patterns and predictions of vulnerable marine benthos across East Antarctica

Here I consider transferability of the model framework developed for HIMI to the continental shelf of East Antarctica and if the model will be suitable for broader application in the development of MPAs for the deep-sea. Using available data, predictions of the distribution and abundance of vulnerable taxa are made and used to assess if a proposed MPA for the region meets CAR principles (comprehensive, adequate and representative) in the context of vulnerable marine taxa.

Chapter 1 - Natural and anthropogenic drivers of the structure and dynamics of sub-Antarctic benthic assemblages

1.1 Abstract

This study provides the first quantitative account of deep-sea benthic communities from the Heard Island and McDonald Islands (HIMI) region. Data were collected by beam trawl from 104 sites throughout HIMI to document the diversity, biomass ($g.m^{-2}$) and distribution of benthic faunal assemblages relative to environmental parameters and disturbance associated with an established bottom fishery. The objective was to understand factors affecting the maintenance and dynamics of HIMI's benthic assemblages under current natural and anthropogenic regimes. A total of 312 taxa from 30,888 individual biomass records were collected from the region, of which 14 taxa were undescribed and likely to be endemic, representing a dramatic increase in the diversity catalogued for HIMI, and indicating that there are important conservation values to maintain. Analyses of taxa biomass using the partitioning around medoids (PAM) clustering method revealed six distinct benthic assemblages. These assemblages defined a clear zonation between HIMI's eastern and western banks, the central plateau, south-facing slopes and waters deeper than 500 meters. The existence of discrete assemblages was best explained by changes in seafloor current speed, temperature and the concentration of particulate organic carbon; variables which are influenced by the east-ward flowing Antarctic Circumpolar Current (ACC) which passes directly across HIMI. There was no association between disturbance from bottom fishing and the structure or distribution of assemblages, despite the extensive bottom fishery that has been operating in the region for more than 10 years. The strong link between environmental parameters and benthic community structure suggests that changes to the Southern Ocean environment, in particular to the ACC, could have dramatic effects on patterns of benthic biodiversity throughout the deep sub-Antarctic.

1.2 Introduction

Over twenty major islands or island groups exist throughout Earth's sub-Antarctic region. Many of these islands have high conservation value, particularly due to their pronounced endemicity and seabird diversity (Clark & Dingwall 1985, Chown *et al.* 2001). Their surrounding marine benthic ecosystems are believed to be rich in species but, like the Antarctic continent, are considered to be particularly susceptible to anthropogenic threats, including bottom fishing (Constable & Holt 2007, Bensch *et al.* 2009) and climate change (IPCC 2007). Despite this, these regions remain poorly described (Clarke *et al.* 2004, Gutt *et al.* 2004, Brandt *et al.* 2007), largely due to the prohibitive cost and logistic difficulties associated with conducting marine research in such isolated areas. Knowledge of the structure and function of these ecosystems is important to allow a better understanding of the biodiversity at risk from these threats and how best to manage these areas.

Australia's sub-Antarctic region includes Macquarie Island in the southwest Pacific Ocean and the Australian Exclusive Economic Zone (EEZ) of Heard Island and McDonalds Islands (HIMI) in the Indian Ocean sector of the Southern Ocean (Fig. 6). The terrestrial environments of these islands have been afforded the highest protection as National Nature Reserves, and the islands, including waters within the territorial sea, i.e. from the low water line to 12 nautical miles (nm) offshore, also have World Heritage Area status (Welsford *et al.* 2011). Both regions support important populations of seabirds and marine mammals, and host established bottom fisheries for Patagonian toothfish, *Dissostichus eleginoides,* or Mackerel Icefish, *Champsocephalus gunnari* (HIMI only). These fisheries have been in operation since the mid-1990s with potential consequences for benthic biota and habitat; an issue magnified by illegal fishing which, until recently, has been a major cause for concern in these regions (Lack 2008, Österblom *et al.* 2015).

Intertidal and offshore waters off Macquarie Island have received some attention, facilitating an assessment of these ecosystems to identified threats (Smith & Simpson 1998, Butler *et al.* 2000a). For HIMI, less than 20 targeted benthic samples, either dredge or grab, have been collected since the late 1800s, and mostly from within the territorial sea in depths less than 200 m where bottom fishing is excluded (Meyer *et al.* 2000, Hureau 2009, Welsford *et al.* 2011). In deep waters beyond the 12 nm territorial sea, data are limited to samples collected incidentally from demersal fish surveys in the early 1990s (Williams & de la Mare 1995) and from by-catch from the HIMI fishery. These incidental qualitative samples provide good spatial coverage, but their analytical value is limited (i.e. presence-only, low taxonomic resolution and gears designed for targeting fish rather than for benthos). Meyer *et al.* (2000) reviewed this data providing some insight into HIMI's benthic habitat. However, the authors acknowledge the constraints of the data, and identified that detailed sampling

would be necessary to evaluate the risk of identified threats like bottom fishing or the impacts of climate change to HIMI's benthic habitat.

Bottom fishing has the potential to alter benthic habitats and patterns of biodiversity (Wassenberg *et al.* 2002, Lokkeborg 2005, Kaiser *et al.* 2006), whereas the ecological implications of climate change remain unclear (Fabry *et al.* 2008, Widdicombe & Spicer 2008). For HIMI, of most concern are recent changes to the eastward-flowing Antarctic Circumpolar Current (ACC). The ACC is the largest current in the Southern Ocean and is integral to global ocean circulation, being the only current that flows completely around the Earth, linking the Atlantic, Pacific and Indian Ocean basins (Orsi *et al.* 1995). The ACC circulation strongly influences regional and global marine biodiversity (Lilley 2008), facilitating a wide circumpolar distribution of many species (Arntz *et al.* 1997) and connectivity among otherwise isolated populations, like HIMI, over large areas of deep water (e.g. Butler *et al.* 2000a, Arntz *et al.* 2006). The Kerguelen Plateau, which encompasses HIMI, constitutes a major barrier to this flow, and as such is likely to affect patterns of biodiversity across the region. However, warming (Gille 2008) and freshening (Helm *et al.* 2010) of the ACC and a significant pole-wards shift in its trajectory (Sokolov & Rintoul 2009) have been observed, with potential ramifications on biota. For instance, the distribution of sessile suspension-feeders, which depends largely on a current driven supply of suspended organic matter (Vinogradov & Tseitlin 1983), may change if the ACC and its associated frontal systems were to shift.

In recognition of HIMI's marine conservation values, and as early mitigation for benthic impacts in the fishery, a substantial marine protected area (MPA; also term the HIMI marine reserve) was developed under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) in October 2002 (IMCRA-Technical-Group 1998, Welsford *et al.* 2011). The MPA includes the World Heritage listed islands and territorial sea, plus an additional marine area extending in parts to the 200 nautical mile EEZ boundary (AAD 2005) (Fig. 6). The design was based on all scientific data available at the time, including biota and geophysical features, with an impetus for CAR (comprehensive, adequate and representative) protection of HIMIs marine conservation values (Meyer *et al.* 2000, Welsford *et al.* 2011). However, the design acknowledged that data on the benthos were particularly sparse, and that additional data would be necessary to confirm whether the marine reserve was achieving CAR protection (Welsford *et al.* 2011).

To redress this paucity of basic information, quantitative benthic samples were collected from 104 sampling stations throughout HIMI at depths between 200 and 1000 m, constituting one of the largest collections of deep-sea benthic fauna from a sub-Antarctic region. These data have since been used in a descriptive manner to refine the MPA boundaries (i.e. description of sample composition

by area) (Hibberd *et al.* 2009, Welsford *et al.* 2011). In this study I take a more quantitative approach by using species biomass compositions to better understand the spatial distribution of distinct assemblages, and to examine associations between environmental parameters (including fishing effort as a proxy for disturbance) and the distribution of those assemblages. Together this data provides baseline information with which to further evaluate the effectiveness of current management regimes and the potential ramifications of bottom fishing and climate change on sub-Antarctic benthic ecosystems.

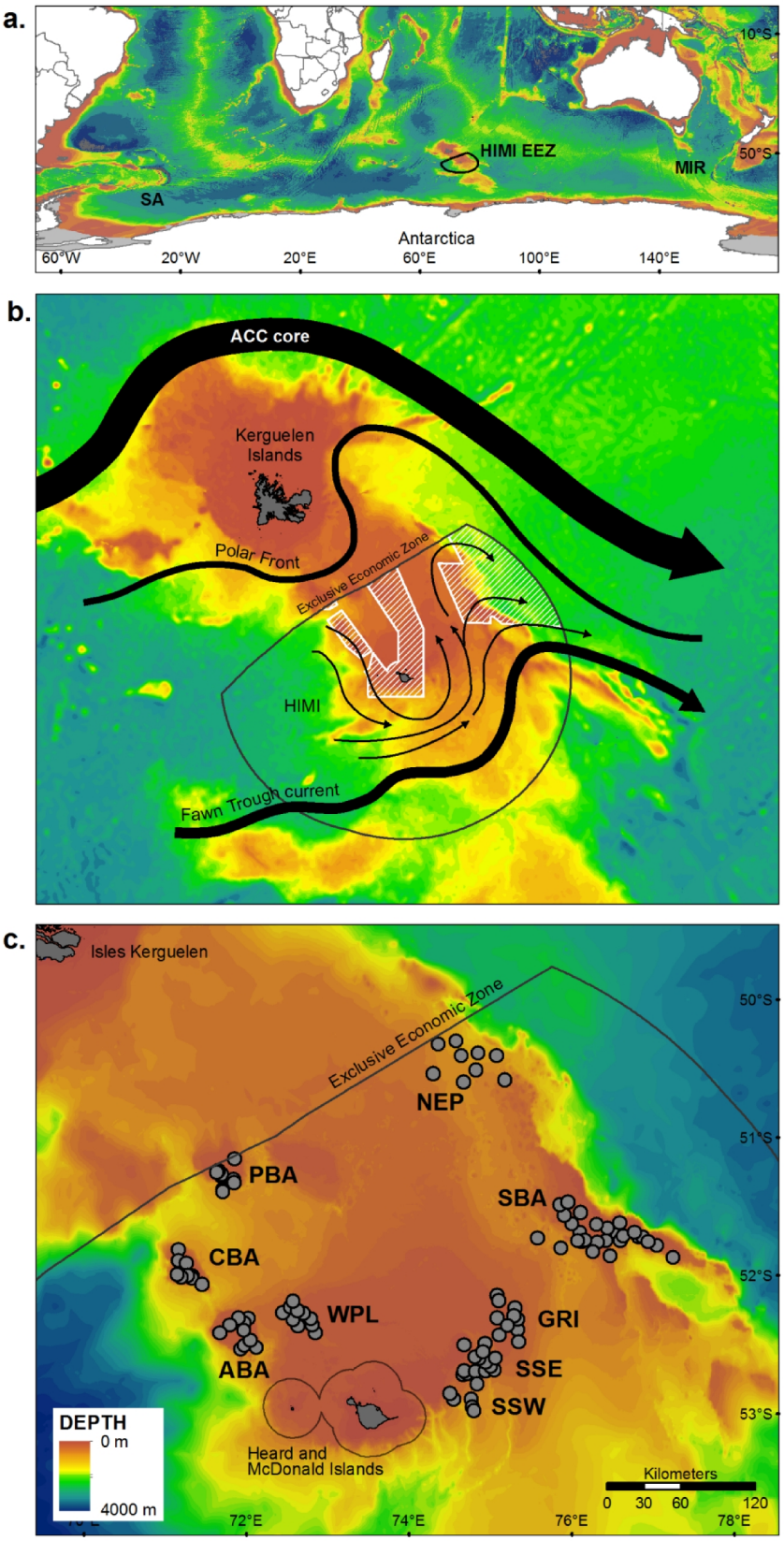

Fig. 6 **(a)** Location of the Kerguelen Plateau and the Australian Exclusive Economic Zone (EEZ) of Heard Island and McDonald Islands (HIMI). The region lies about 1,500 kilometres north of Antarctica and over 4,000 kilometres south-west of Western Australia at roughly 53°S and 73°E. Other seascape features which span a high latitudinal range include the Scotia Arc (SA) and Macquarie Island Ridge (MIR). Depth sourced from GEBCO (GEBCO_08 2008). **(b)** Schematic of the circulation pattern over and around the northern Kerguelen Plateau interpreted from Park *et al.* (2008b) and van Wijk *et al.* (2010). Most of the ACC transport (~100 sverdrup (Sv), 1 Sv = 10^6 m^3 s^{-1}) is deflected north of the Kerguelen Islands (KI), but a substantial (30 – 40 Sv) remainder passes through the Antarctic Zone between KI and Antarctica (Park *et al.* 2008b). The Fawn Trough south of Heard Island constitutes a favoured zonal passage for the circumpolar flow crossing the plateau (Park *et al.* 1991, Park & Gambe´roni 1997, Roquet *et al.* 2009). Thin black arrows denote the circulation pattern throughout HIMI. These flows are intensified on HIMI's western and southern slopes (van Wijk *et al.* 2010). The HIMI MPA, as refined in March 2014, is identified by the white hashed area**.** Depth sourced from GEBCO (GEBCO_08 2008). **(c)** The location of the 104 benthic sampling stations throughout the HIMI EEZ. Geographic areas sampled included Aurora (ABA), Coral (CBA), Pike (PBA) and Shell Banks (SBA), Northeast (NEP) and Western Plateau (WPL), Gunnari Ridge (GRI), and Southern Slope East (SSE) and West (SSW). HIMI's territorial waters are identified by the hashed area surrounding the islands. Depth sourced from the Kerguelen Digital Elevation Model (Beaman & O'Brien 2011).

1.3 Methods

1.3.1 Benthic invertebrate data

Sampling of the benthic habitat within the HIMI EEZ was undertaken across nine geographic areas, selected for the purpose of evaluating regional differences in faunal composition, and to encompass the range of environments and geomorphologies present between 200 and 1000 m depth (Fig. 6c). They included Aurora Bank (ABA), Coral Bank (CBA), Pike Bank (PBA), Shell Bank (SBA), Northeast Plateau (NEP), Southern Slope West (SSW), Southern Slope East (SSE) and two areas representative of the greater central plateau region, including Western Plateau (WPL) and Gunnari Ridge (GRI). Physical characteristics of these areas and the rationale behind their selection are outlined in Table 2. These areas were sampled between 2003 and 2008 over three sampling campaigns from the FV *Southern Champion*. Nine to ten stations were randomly sampled in all areas except Shell Bank due to reasons outlined in Table 2. Samples were collected using a 2.7 m wide beam trawl fitted with a 1 cm^{-2} net mesh.

Samples were sorted into broad taxonomic groups onboard the sampling vessel and then frozen for later analysis. In the laboratory, samples were defrosted and then sieved over a 1 cm mesh prior to sorting and classification. All organisms retained on the sieve were sorted into species, if known, or in most case operational taxonomic units (OTU) representative of a species (e.g. Demospongiae sp1) or a group of species (i.e. Demospongiae spp.). For further information on the use and definition of OTUs see Blaxter *et al.* (2005). Where possible, OTUs were later separated into species or lower taxonomic groups (i.e. family or class) with the assistance of expert taxonomists (see Acknowledgements). Group OTUs remain for demosponges, hydroids and bryozoans due to difficulties with separating these groups after damage received in sample collection and retrieval. Finally, identified species and OTUs were categorized according to their mobility (sessile or mobile) and feeding mode (suspension-feeders, scavengers, predators, deposit-feeders and grazers) by consulting Fauchald and Jumars (1979) for polychaetes, Short and Potter (1987) for molluscs, and Barnes (1987) and Macdonald *et al.* (2010) for all remaining phyla. Hereafter, 'taxa' will be used to refer to identified species and OTUs.

Individuals of all non-colonial taxa were counted and then weighed collectively, while colonial taxa were only weighed. Counts and weights were standardised to abundance (number of individuals) and biomass (grams) per square metre of the seafloor ($n.m^{-2}$ and $g.m^{-2}$, respectively) using swept area (m^{-2}). Swept area, i.e. the area of seafloor sampled by each trawl, was determined by multiplying trawl

distance by the beam trawl width, 2.7 m. Trawl distance was calculated as the great circle distance from the start and finish coordinates, which were determined from line tension and vessel position.

1.3.2 Environmental variables and fishing effort

Nineteen abiotic variables with coverage across HIMI were utilized to define six predictor categories (Table 3). Categories included (1) sea surface properties relating to phytoplankton productivity, including estimates of particulate organic carbon, the major food supply to benthic communities (Vinogradov & Tseitlin 1983), (2) bottom water properties characterising seafloor habitats, (3) physical properties relating to seabed structure and relief, (4) distance as a proxy to point source influences (i.e. canyons), (5) water depth and (6) fishing effort as a proxy for disturbance to the seafloor habitats.

Water depth, slope and aspect were compiled from the Kerguelen digital elevation model (KDEM), on a 0.01-degree bathymetric grid (ca. 1000 m) (Beaman & O'Brien 2011). Slope and aspect were calculated from the KDEM using spatial analyst procedures in software package ArcGIS version 10.1, ESRI, USA. All other layers were reclassified to a consistent 0.1-degree grid. Values for all variables were extracted at the midpoint (latitude/longitude) of each beam trawl track.

Fishing effort at each benthic sampling station was determined based on all fishing events since the commencement of the HIMI bottom fishery in 1997. Details for each fishing event since this time, including date, haul start and end coordinates, and gear type (demersal trawl, net or longline), were available from the Australian Antarctic Division (AAD) and enabled the level of fishing effort at each station to be calculated using procedures developed by Welsford *et al.* (2014b). Briefly, all individual fishing events were projected as straight lines according to their start and finish coordinates using R (R Development Core Team 2010). In some instances fishing events may not be in a straight line, however for the purposes of this analysis it was assumed that a line drawn between the reported start and finish coordinates was the best approximation for the location of the gear on the seafloor (Welsford *et al.* 2014b). A virtual 3 x 3 km grid was then projected across HIMI to encompass these fishing events, and effort summarised by grid cell using a series of 'cookie-cutting' procedures to excise the area that had experienced one fishing event, two fishing events to *n* fishing events, taking into account overlapping events. Total effort per cell was expressed as the sum of these areas (km^2). Fishing effort per sampling station was then extracted from this virtual effort grid at the midpoint of each beam trawl track. Only fishing events that occurred prior to benthic sample collections were considered.

Table 2 Physical characteristic of the geographic areas sampled throughout the HIMI region and the rationale behind their selection, including the total number of samples collected and their collective swept area (SA), i.e. total area of seafloor sampled at each area. Depth was determined from the Kerguelen Digital Elevation Model (KDEM) (Beaman & O'Brien 2011). Geomorphology is described with reference to (i) geomorphic types defined by Heap and Harris (2008), (ii) the KDEM, (iii) regional descriptions from Meyer *et al.* (2000), (iv) sediment data collected from the Ocean Drilling Program (ODP 1998), video observations of the seafloor (Kilpatrick *et al.* 2011) and (v) sample observations.

Geographic area	Short	Samples	SA (m^2)	Depth (m)	Geomorphology	Rational
Aurora Bank	ABA	10	21143	222-370	Large, relatively flat, mesa-like bank rising steeply from deep water. Top is rugose with small pinnacles, boulders and a covering of sand.	Situated southeast of CBA and west of WPL. Sampled to compare with these and the eastern banks.
Coral Bank	CBA	10	21143	222-370	Relatively flat, mesa-like bank rising steeply from deep water. Top is rugose with small pinnacles, boulders and a covering of sand.	Sampled to compare with nearby ABA, PBA and the eastern banks.
Pike Bank	PBA	9	22335	246-756	Flat topped bank with relatively steep eastern slopes. Flat on top but pebbly and gnarly on the slopes.	Situated northeast of CBA and targeted by commercial fishing.
Shell Bank	SBA	27	101599	212-779	Large, relatively flat, mesa-like bank surrounded by steep, craggy slopes, particularly to the east. White sand and thick shell grit deposit unique to area. Fine grey sand and silt in deeper waters toward the trough to the west.	SBA was first sampled in 2003. At this time, it was debatable whether the southern end of the bank should be included in the MPA. Hence, SBA was divided into northern and southern sections, and 10 samples were targeted from each area. A preliminary analysis of these samples indicated high habitat heterogeneity. Hence further sampling was conducted in 2007 to confirm this community pattern, and the conservation value of this elongated bank.
Northeast Plateau	NEP	9	34892	594-970	Plateau seascape sloping into deeper water in the east. Hard substratum with cobbles, yellow sand and grey silt.	Representative of a deep plateau community in proximity to SBA.
Southern Slope West	SSW	10	25313	288-941	South-facing slope boarding the central plateau area with generally steep and undulating craggy slopes. Mostly medium-grain black basaltic sand, grey silt and cobble.	A complex oceanographic and topographic area that is targeted by commercial fishing. Comparable to shelf break and continental slope depths elsewhere in the world.
Southern Slope East	SSE	10	25313	168-558	Broad, flat and even south-facing slope with moderate and undulating geomorphology. Mostly smooth, medium-grain black basaltic sand, grey silt and cobble. Top graduating into plateau-type habitat similar to WPL and GRI.	Neighbouring SSW, but with negligible fishing effort.
Western Plateau	WPL	10	21987	264-462	Broad, flat and even plateau terrain. Mostly smooth, medium-grain black basaltic sand and grey silt.	Part of the greater central plateau and chosen as a reference zone as it is in a comparable depth range to ABA and CBA.
Gunnari Ridge	GRI	10	24816	218-334	Broad, flat and even plateau/ridge. Mostly smooth, medium-grain black basaltic sand and grey silt.	South eastern corner of the central plateau and targeted by commercial fishing; mostly pelagic.

Table 3 Datasets of environmental predictor variables across HIMI.

Variable	Short	Unit	Variable layer description	Reference
Surface water				
Chlorophyll *a*	chl	mg m^{-3}	Average of annual values from the MODIS (Moderate Resolution Imaging Spectroradiometer) aqua mission data from July 2009 to December 2008.	Feldman and McClain (2010)
Sea surface temperature	sst	°C		
Mixed layer depth	mld	m	Annual mean concentration derived from the CSIRO Atlas of Regional Seas (CARS 2009).	Condie and Dunn (2006)
Particulate organic carbon	poc	mg m^{-3}	Average of annual values from the MODIS aqua mission data from July 2009 to December 2008.	Stramski *et al.* (2008)
Bottom water				
Temperature	btm.tmp	°C	Annual mean concentration derived from CARS 2009.	Ridgway *et al.* (2002)
Dissolved oxygen	btm.oxy	ml l^{-1}		
Nitrate	btm.nit	µmol l^{-1}		
Phosphate	btm.pho	µmol l^{-2}		
Silicate	btm.sil	µmol l^{-1}		
Salinity	btm.sal	PPS		
Physical				
Seafloor current speed	btm.spd	m s^{-1}	Current speed near the seafloor averaged over 12 snapshots from the CAISOM ocean model.	Galton-Fenzi *et al.* (2012)
Seafloor vertical velocity	btm.vvl	m s^{-1}	Vertical velocity at the seafloor averaged over 12 snapshots from the CAISOM ocean model.	
Seafloor slope	slope	m	Slope values calculated from the Kerguelen Digital Elevation Model (KDEM).	Beaman and O'Brien (2011)
Seafloor aspect	aspect	m	Aspect values calculated from the KDEM.	
Distance				
Distance to sub-Antarctic island	dist.isl	km	Distance to nearest land mass north of 65°S calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km.	Australian Antarctic Data Centre (AADC)
Distance to canyon axe	dist.can	km	Distances to nearest canyon axis calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from O'Brien and Post's (2009) seafloor geomorphology data.	AADC, O'Brien *et al.* (2009)
Distance to shelf break	dist.shf	km	Distance to nearest area of sea floor of depth 500 m or less. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from ETOPO1 bathymetry data.	AADC, Smith and Sandwell (1997)
Water depth				
Depth	depth	m	Depth estimated from the KDEM.	Beaman and O'Brien (2011)
Fishing effort				
Fishing effort	effort	km^2	Total fishing effort per cell expressed as the sum of area impacted by one fishing event, two fishing events to *n* fishing events. Only fishing events that occurred prior to benthic sample collections were considered.	Welsford *et al.* (2014b)

1.3.3 Statistical analysis

The existence of distinct assemblages throughout HIMI, and how these assemblages relate to their environment, was evaluated using taxa biomass data ($g.m^{-2}$). Biomass has been used successfully for classification of benthic trawl data (Ward *et al.* 2006b), and was chosen over abundance due to the dominance of colonial forms like sponges and corals at most stations throughout HIMI.

Patterns in the multivariate biomass data were evaluated by the clustering method Partitioning Around Medoids (PAM) (Kaufman & Rousseeuw 1990) in R using the package *cluster* (Maechler *et al.* 2015). Taxa biomass for each station was forth-root transformed, so as to minimize the undue influence of a few large/heavy taxa on the analyses (Field *et al.* 1982), and a similarity matrix was constructed based on the Bray–Curtis (BC) dissimilarity metric. PAM requires that we specify the number of clusters (k) that will be formed in advance. To determine the optimal number of clusters (i.e. assemblages) PAM solutions for k = 2, 3, …, 10 groups were calculated for the BC matrix, and evaluated using the Calinski-Harabasz criterion (CH_k) (Calinski & Harabasz 1974) as a measure of the cohesion between the partition and the data set for a given k (Milligan & Cooper 1985). The optimal number of assemblages is then defined as a value of k that maximizes CH_k. The dissimilarity between stations, and the optimal PAM cluster solution(s), was visualised using non-metric multidimensional scaling (nMDS) plots. Differences in faunal composition between assemblages and specific discriminator taxa (see below) were detected using Similarity Percentage Analysis (SIMPER) (Clarke 1993, Clarke & Warwick 2001) in PRIMER v6.1.12 with the add-on PERMANOVA+ v1.0.2 (Clarke & Gorley 2006). Discriminator taxa were defined as those contributing >5% to among-group dissimilarity and with a high dissimilarity to standard deviation ratio (Diss/SD > 1.5). Analysis of Similarity (ANOSIM) tests (Clarke 1993) were used to evaluate differences between assemblages in regards to biomass and species richness S (i.e. number of taxa) per station.

The extent to which environmental variables accounted for the observed assemblage pattern was analysed using non-parametric multivariate multiple regressions by means of the *distLM* function in PERMANOVA+ (McArdle & Anderson 2001). Selected variables were analyzed separately for their relationship with the transformed taxa biomass data, and variables were then subjected to a step-wise forward-selection procedure to model the percentage of overall variation in benthic assemblage structure accounted for by the environmental variables of interest. Distance-based redundancy analysis (dbRDA) bi-plots were generated to visualise the direction and magnitude of the relationship between individual predictor variables and the multivariate community pattern (Legendre & Anderson 1999).

Environmental variables were normalized to a common scale after log transformation of skewed variables. Variable selection for inclusion in multivariate analyses was determined by examining pairwise linear regressions between all normalized variables to account for caveats associated with (multi)collinearity as regression-based models are sensitive to correlations between factors. Variables with Pearson's correlation values $|r| > 0.85$ (Anderson *et al.* 2008) were considered collinear, and only one of a group of collinear variables was included in the analysis. Such correlations were found between *poc* and *chl*, and *dist.isl*, *dist.can* and *mld* (abbreviations as per Table 3). Of these groups of collinear variables, *poc* and *dist.isl* were retained; *poc* for its relevance to benthic productivity at the seafloor and *dist.isl* as a proxy for distance to islands.

1.4 Results

1.4.1 Biodiversity

A total of 312 taxa from 13 phyla were collected from the 104 stations across HIMI, including 14 undescribed or new species which are likely to be endemic to the region (Table 4). The mean biomass per station was 10.32 g.m^{-2} (range = <0.01 – 181.60 g.m^{-2}) and the average species richness was 40 taxa per station (range = 2 – 79 taxa per station). Echinoderms, molluscs and cnidarians were the top contributors to diversity and the dominant phyla in terms of biomass were poriferans and echinoderms, which together accounted for >70% of the average faunal biomass per square metre of seafloor (Table 5). Echinoderms were the most widely distributed and abundant fauna, present at all stations and contributing on average 60% of the total abundance of non-colonial taxa. Other important contributors to biomass or abundance were the annelids, bryozoans, ascidians, cnidarians, molluscs and crustaceans. For some groups, like Demospongiae, diversity was underrepresented due to the coarse taxonomic resolution used here. Pycnogonids and holothurians made up the majority of undescribed taxa (n = 6 taxa per group), however only these groups were scrutinized in sufficient detail by relevant experts to determine valid undescribed species. Greater scrutiny of other benthic taxa would most likely reveal much higher diversity and numbers of undescribed/endemic species. Nonetheless, cumulative species observations for taxa present at 2 or more stations (n = 249) reached an asymptote at approximately 85 stations/samples (Fig. 7), suggesting that sampling was effective at representing the local diversity for those well identified groups.

Individually most taxa occurred at few stations. Sixty-three taxa were restricted to only 1 station (i.e. station-restricted), another 137 were exceedingly rare (i.e. < 10% of stations), and a further 82 were local (10 – 30% of stations). The remaining 30 taxa were wide-spread across HIMI, present at > 30% of stations, the most abundant being the ophuroids *Ophiurolepis carinata* followed by *Ophiuroglypha ambigua* (Table 4). Many colonial taxa like Demospongiae spp., Hydrozoa spp., and Bryozoa spp. were also widespread, present at more than 70% of stations, although the coarse taxonomic resolution used here may well mask evidence of endemism or restricted distributions of individual species.

The predominant feeding mode was suspension feeding (167 taxa), followed by predators/scavengers (75 taxa), detritivores (34 taxa), deposit-feeders (22 taxa) and grazers (14 taxa). Suspension-feeders made up 77.30% (1.07 g.m^{-2}) of the average biomass per square meter of seafloor, most being sessile. Predators accounted for 16.08% (0.22 g.m^{-2}), detritivores 6.01% (0.08 g.m^{-2}), deposit-feeders 0.62% (0.008 g.m^{-2}) and grazers 0.02% (0.0003 g.m^{-2}).

Table 4 List of taxa identified from the 104 stations across HIMI including their average biomass (transformed, $g.m^{-2}$, ± standard error) and presence (total records and percentage (% in parentheses) occurrence across all 104 stations) per assemblage. Assemblages were identified using the partioning around mediods (PAM) clustering method of taxa biomass data. * Taxa potentially undescribed or endemic.

			ASSEMBLAGE					
Taxa	**Biomass**	**Presence**	1	2	3	4	5	6
PORIFERA								
Demospongiae								
Latrunculia spB	0.4902 ± 0.136	13 (12.5)	0.267	0.17	0.0557	0.0264	0.0309	
Porifera spAK	0.319 ± 0.319	1 (0.96)		0.0376				
Porifera spAO	0.0112 ± 0.004	8 (7.69)	0.11		0.0113	0.0488	0.0085	
Porifera spL	0.0789 ± 0.0176	20 (19.23)	0.3395	0.1434	0.0345	0.0208	0.0429	
Porifera spU	0.0069 ± 0.0049	2 (1.92)		0.0275				
Stylocordyla borealis	0.0244 ± 0.0057	18 (17.31)	0.1046	0.1544	0.0385		0.0237	
Suberites caminatus	0.0283 ± 0.0076	14 (13.46)	0.2408	0.0158	0.0816	0.0574	0.0055	
Tetilla leptoderma	2.6296 ± 0.5061	27 (25.96)	0.5543	0.7492	0.1937		0.0695	
Demospongiae	3.4051 ± 0.3589	90 (86.54)	2.2551	0.9635	0.6809	0.7733	0.4897	0.01
Hexactinellida								
Hexactinellida spA	0.7642 ± 0.1709	20 (19.23)		0.3844	0.2837		0.0091	
Hexactinellida spp.	6.3079 ± 1.2876	24 (23.08)	1.4495	0.1927	0.0489	0.0583	0.0065	
CNIDARIA								
Actinaria								
Actinaria spA	0.0203 ± 0.0049	17 (16.35)	0.0632	0.0501	0.0143	0.0864	0.0485	
Actinaria spB	0.0052 ± 0.0037	2 (1.92)		0.0096			0.0088	
Actinaria spC	0.1401 ± 0.034	17 (16.35)		0.091			0.1855	
Actinaria spD	0.1616 ± 0.0404	16 (15.38)	0.0707	0.0204	0.0378	0.019	0.193	
Actinaria spE	0.1937 ± 0.1937	1 (0.96)					0.019	
Actinaria spF	0.0069 ± 0.0026	7 (6.73)		0.0124	0.0638		0.0146	
Actinaria spH	0.2074 ± 0.1037	4 (3.85)	0.1025			0.0673	0.0229	
Actinaria spI	0.0093 ± 0.0046	4 (3.85)			0.0409	0.0264		
Actinaria spK	0.0025 ± 0.0018	2 (1.92)					0.0126	
Actinaria spL	0.0176 ± 0.0176	1 (0.96)	0.052					
Actinaria spM	0.0013 ± 0.001	2 (1.92)				0.0139	0.0048	
Actinostolidae sp1	0.0044 ± 0.0044	1 (0.96)					0.0074	
Bolocera sp1	0.1585 ± 0.0915	3 (2.88)		0.0136			0.0321	
Capnea georgiana	0.0226 ± 0.0113	4 (3.85)				0.0084	0.0308	
Hormathiidae sp	0.1115 ± 0.0263	18 (17.31)		0.0772	0.0277	0.0183	0.168	
Glyphoperidium bursa	0.3333 ± 0.1005	11 (10.58)			0.0632		0.1501	0.0637
Liponema sp1	0.1238 ± 0.0253	24 (23.08)		0.0628	0.0142	0.077	0.3042	
Alcyonacea								
Cnidaria sp14	0.0007 ± 0.0007	1 (0.96)			0.0091			
Cnidaria sp16	0.0062 ± 0.0013	22 (21.15)	0.0661	0.0072	0.0963		0.0664	0.0185
Cnidaria sp17	0.0077 ± 0.0024	10 (9.62)		0.0124	0.0051	0.0073	0.0518	
Cnidaria sp18	0.0055 ± 0.0017	10 (9.62)	0.0541	0.0147	0.0097		0.0391	
Cnidaria sp20	0.0214 ± 0.0123	3 (2.88)		0.018			0.0172	
Cnidaria sp21	0.0003 ± 0.0003	1 (0.96)					0.0036	
Cnidaria sp25	0.0292 ± 0.013	5 (4.81)		0.0131	0.0514	0.0181	0.0108	
Cnidaria sp30	0.0128 ± 0.0031	17 (16.35)		0.0284	0.0101	0.0637	0.0584	
Cnidaria sp35	0.0006 ± 0.0003	4 (3.85)					0.0169	
Cnidaria sp42	0.0876 ± 0.0438	4 (3.85)	0.1095	0.0285				
Cnidaria sp43	0.0038 ± 0.0013	9 (8.65)	0.0503	0.032	0.0188		0.0141	
Cnidaria sp52	0.0007 ± 0.0007	1 (0.96)						0.0183
Cnidaria sp55	0.0001 ± 0.0001	1 (0.96)				0.0068		
Cnidaria sp58	0.0054 ± 0.0018	9 (8.65)			0.0229		0.0425	
Cnidaria sp6	0.011 ± 0.0026	18 (17.31)	0.1269	0.017	0.046	0.0257	0.0593	
Cnidaria sp62	0.0052 ± 0.0037	2 (1.92)			0.0123	0.0199		
Cnidaria sp64	0.009 ± 0.0064	2 (1.92)			0.0202		0.0044	
Cnidaria sp68	0.0478 ± 0.0478	1 (0.96)	0.0668					
Cnidaria sp70	0.2034 ± 0.2034	1 (0.96)					0.0192	
Cnidaria sp72	0.0254 ± 0.0127	4 (3.85)					0.0424	
Ceriantharia								
Ceriantharia spA	0.0023 ± 0.0006	15 (14.42)	0.0432		0.0241	0.0579	0.0282	

			ASSEMBLAGE					
Taxa	**Biomass**	**Presence**	1	2	3	4	5	6
Ceriantharia spB	0.0032 ± 0.0011	8 (7.69)			0.0251	0.0833		
Gorgonacea								
Cnidaria sp1	0.0078 ± 0.0018	18 (17.31)		0.0929	0.0583	0.0427	0.0056	
Cnidaria sp2	0.0109 ± 0.0021	26 (25)	0.1543	0.0566	0.0363	0.1102	0.0189	0.0135
Cnidaria sp24	0.0112 ± 0.003	14 (13.46)	0.0741	0.0267	0.0294	0.0841	0.0095	0.0142
Cnidaria sp29	0.0004 ± 0.0001	12 (11.54)		0.0081	0.0054	0.0132	0.0279	0.01
Cnidaria sp3	0.0022 ± 0.0009	6 (5.77)		0.0095	0.0216	0.0043	0.0024	0.0055
Cnidaria sp34	0.0013 ± 0.0013	1 (0.96)		0.0096				
Cnidaria sp4	0.0108 ± 0.0016	48 (46.15)	0.3499	0.1969	0.1224	0.1162	0.0285	
Cnidaria sp45	0.002 ± 0.002	1 (0.96)		0.0105				
Cnidaria sp59	0.0282 ± 0.0163	3 (2.88)			0.0113	0.0334	0.0107	
Cnidaria sp65	<0.0001	1 (0.96)				0.0045		
Hydrocorallia								
Hydrocorallia spp.	0.0488 ± 0.0122	16 (15.38)	0.0957		0.0342	0.2503	0.0285	
Hydrozoa	0.1541 ± 0.0165	87 (83.65)						
Hydrozoa spp.	0.1541 ± 0.0165	87 (83.65)	0.9872	0.1517	0.2306	0.2989	0.3112	0.0873
Pennatulacea								
Ceriantharia spC	0.0008 ± 0.0008	1 (0.96)					0.0049	
Pennatulacea spC	0.0091 ± 0.0091	1 (0.96)				0.0206		
Scleractinia								
Cnidaria sp40	0.0055 ± 0.0012	20 (19.23)		0.0063	0.0615	0.1298	0.0231	
Flabellum spA *	0.0218 ± 0.0044	25 (24.04)		0.0105	0.0496	0.0395	0.1626	0.0244
Zooanthid								
Cnidaria sp19	0.0032 ± 0.0013	6 (5.77)		0.01		0.0285	0.015	
Cnidaria sp23	0.0011 ± 0.0007	3 (2.88)		0.0096	0.0117		0.0027	
PLATYHELMINTHES								
Polycladida spB	0.0016 ± 0.0009	3 (2.88)			0.0083		0.0109	
Polycladida spC	0.0073 ± 0.0052	2 (1.92)					0.0161	
PRIAPULA								
Priapulidae spA	0.0034 ± 0.002	3 (2.88)		0.012			0.0138	
SIPUNCULIDA								
Sipuncula spA	0.0005 ± 0.0003	2 (1.92)		0.0058			0.0048	
Sipuncula spB	0.0001 ± 0.0001	1 (0.96)				0.007		
Sipuncula spC	0.0015 ± 0.0015	1 (0.96)					0.0056	
Sipuncula spD	0.0013 ± 0.0013	1 (0.96)	0.0274					
Sipuncula spE	0.1301 ± 0.1301	1 (0.96)					0.0172	
Sipuncula spF	0.0514 ± 0.0514	1 (0.96)					0.0136	
MOLLUSCA								
Bivalvia								
Arcidae spA	0.0082 ± 0.0058	2 (1.92)	0.0511			0.005		
Bivalvia spE	0.0388 ± 0.0275	2 (1.92)	0.1135					
Cardiidae spA	<0.0001	1 (0.96)					0.002	
Cardiidae spB	0.0001 ± 0.0001	2 (1.92)			0.0102			
Crassatellidae spA	0.0057 ± 0.0018	10 (9.62)		0.0228			0.0584	
Crassatellidae spB	0.0002 ± 0.0001	6 (5.77)		0.0058	0.0143	0.0081	0.0057	
Cuspidaria spA	0.002 ± 0.0008	6 (5.77)			0.0163		0.0215	
Cuspidariidae spA	0.0002 ± 0.0001	2 (1.92)			0.004		0.0037	
Cyamiidae spA	0.0002 ± 0.0001	9 (8.65)			0.0258	0.007	0.0111	
Cyamiidae spB	<0.0001	2 (1.92)			0.0033		0.0013	
Cyclopecten spA	0.0001	8 (7.69)	0.0197	0.0112		0.0055	0.004	
Euciroa spA	<0.0001	2 (1.92)		0.004		0.0055		
Galeommatidae spA	0.0034 ± 0.0024	2 (1.92)	0.0411		0.0044			
Gouldia (Gouldiopa) spA	0.0003 ± 0.0001	5 (4.81)			0.0056	0.0066	0.0073	
Hiatella spA	0.0217 ± 0.004	29 (27.88)	0.4096	0.0686	0.022	0.0635	0.0112	
Hochstetteria meridionalis	<0.0001	1 (0.96)		0.0035				
Kidderia spA	<0.0001	1 (0.96)		0.0024				
Laternula spA	0.1107 ± 0.0286	15 (14.42)				0.0182	0.1775	
Limopsidae spA	0.0009 ± 0.0002	29 (27.88)	0.1768	0.0551	0.0537	0.0208	0.0076	
Limopsidae spB	0.0026 ± 0.0004	38 (36.54)	0.2508	0.0585	0.1013	0.0401	0.0048	
Limopsidae spC	0.0001 ± 0.0001	1 (0.96)			0.0055			
Limopsidae spE	0.0039 ± 0.0009	18 (17.31)	0.1352	0.0223	0.034	0.032	0.023	

			ASSEMBLAGE					
Taxa	**Biomass**	**Presence**	1	2	3	4	5	6
Nuculana spA	0.0009 ± 0.0009	1 (0.96)					0.005	
Nuculana spB	0.0003 ± 0.0003	1 (0.96)					0.0037	
Ostreidae spA	0.0002 ± 0.0001	7 (6.73)		0.0096	0.0274		0.0021	
Psammobiidae spA	0.0057 ± 0.0026	5 (4.81)					0.0327	
Ungulinidae spA	0.0008 ± 0.0005	3 (2.88)			0.0053		0.0096	
Gastropoda								
Buccinidae spA	0.0022 ± 0.0007	9 (8.65)	0.0179		0.0033		0.0436	
Buccinidae spB	0.0264 ± 0.0061	19 (18.27)		0.0215	0.016		0.1722	
Buccinidae spC	0.0072 ± 0.0019	15 (14.42)	0.0422		0.0105		0.0945	
Buccinidae spE	<0.0001	1 (0.96)			0.0041			
Cancellariidae spA	0.0004 ± 0.0002	3 (2.88)				0.0156	0.0049	
Cancellariidae spB	0.0002 ± 0.0001	3 (2.88)			0.0047		0.0067	
Cerithiopsidae spA	<0.0001	1 (0.96)		0.003				
Cerithiopsidae spB	<0.0001	1 (0.96)					0.0019	
Enixotrophon spA	0.0016 ± 0.0007	6 (5.77)		0.0093			0.0279	
Enixotrophon spB	0.0119 ± 0.0084	2 (1.92)		0.0194			0.0055	
Enixotrophon spC	0.0003 ± 0.0001	4 (3.85)					0.0135	
Epitoniidae spA	0.0012 ± 0.0005	5 (4.81)		0.0046		0.0073	0.0133	
Fasciolariidae spB	0.0001	2 (1.92)			0.0051	0.0055		
Fasciolariidae spC	<0.0001	1 (0.96)			0.0045			
Fusitriton aurora	0.0011 ± 0.0004	6 (5.77)					0.0304	
Gastropoda spA	0.0005 ± 0.0004	2 (1.92)		0.0084	0.007			
Gastropoda spB	0.0023 ± 0.0006	15 (14.42)	0.0873		0.0103	0.0225	0.0299	
Gastropoda spF	0.0002 ± 0.0002	1 (0.96)					0.0032	
Gastropoda spO	<0.0001	1 (0.96)				0.0054		
Icuncula spA	0.0009 ± 0.0004	6 (5.77)	0.0357		0.0034	0.0131	0.0063	
Nassariidae spA	0.0004 ± 0.0004	1 (0.96)			0.0077			
Naticidae spA	0.0051 ± 0.001	24 (23.08)		0.0083	0.0743		0.1094	
Naticidae spB	0.002 ± 0.0014	2 (1.92)	0.0357				0.002	
Provocator pulcher	0.0387 ± 0.0081	23 (22.12)		0.0411	0.1033	0.1316	0.1041	
Rissoidea spA	<0.0001	3 (2.88)			0.0071		0.0013	
Terebridae spA	0.0003 ± 0.0002	2 (1.92)	0.0183				0.0037	
Trichotropis spA	0.0023 ± 0.0009	6 (5.77)	0.0615	0.015		0.0136	0.0035	
Trochidae spA	0.0024 ± 0.0006	17 (16.35)			0.0118	0.0088	0.0843	
Trochidae spB	0.0001	5 (4.81)	0.0179		0.0043		0.0074	
Turridae spA	0.0146 ± 0.0044	11 (10.58)		0.012	0.0437	0.0167	0.0507	
Turridae spB	<0.0001	1 (0.96)				0.0047		
Turridae spC	0.0001 ± 0.0001	1 (0.96)					0.0031	
Turridae spD	0.0001 ± 0.0001	1 (0.96)					0.0031	
Turridae spE	<0.0001	1 (0.96)					0.0014	
Turridae spF	<0.0001	2 (1.92)			0.0077			
Turridae spG	<0.0001	2 (1.92)			0.0021		0.0017	
Octopoda								
Benthoctopus levis	0.2088 ± 0.0445	22 (21.15)	0.1642	0.0776	0.0787	0.3309	0.0652	
Graneledone antarctica	0.3029 ± 0.0913	11 (10.58)	0.1515		0.0742	0.196	0.0542	
Opisthobranchia								
Austrodoris kerguelenensis	0.003 ± 0.0009	11 (10.58)		0.0302	0.0373		0.0184	
Bathydoris spA	0.022 ± 0.0127	3 (2.88)	0.0722			0.0064	0.0047	
Lamellariidae spA	0.0002 ± 0.0001	7 (6.73)		0.0096	0.0094	0.0086	0.007	
Opistobranchia spA	0.0555 ± 0.0555	1 (0.96)					0.0139	
Opistobranchia spB	0.0012 ± 0.0007	3 (2.88)			0.0278			
Opistobranchia spC	0.0001 ± 0.0001	1 (0.96)					0.0024	
Opistobranchia spE	0.0002 ± 0.0001	2 (1.92)					0.006	
Opistobranchia spF	0.0007 ± 0.0005	2 (1.92)					0.0092	
Opistobranchia spG	0.0009 ± 0.0004	7 (6.73)			0.0191		0.019	
Opistobranchia spJ	0.0001 ± 0.0001	1 (0.96)				0.0061		
Patellogastropoda								
Fissurellidae spA	0.0006 ± 0.0002	9 (8.65)	0.0621	0.003	0.011	0.0208	0.0023	
Nacella spA	0.0009 ± 0.0003	7 (6.73)	0.0644		0.0078	0.0041	0.0058	

Taxa	Biomass	Presence	ASSEMBLAGE 1	2	3	4	5	6
Polyplacophora								
Leptochiton kerguelenensis	0.001 ± 0.0003	10 (9.62)	0.0687	0.0092	0.0049	0.0498		
Polyplacophora spA	0.0002 ± 0.0001	7 (6.73)		0.0275	0.0106			
Scaphopoda								
Dentalium aegeum	0.0281 ± 0.0057	24 (23.08)	0.0487		0.028		0.1422	
ANNELIDA								
Polychaeta	0.0379 ± 0.0057	44 (42.31)						
Polychaeta spp.	0.0379 ± 0.0057	44 (42.31)	0.4966	0.0084	0.0551	0.144	0.159	0.0885
Aphroditidae spA	0.154 ± 0.0235	43 (41.35)	0.0686	0.0434	0.1097	0.0454	0.4727	
Serpula spA	1.1571 ± 0.1393	69 (66.35)	1.4928	0.1243	0.2974	0.245	0.2058	0.0134
BRYOZOA								
Bryozoa spp.	0.9427 ± 0.1111	72 (69.23)						
BRACHIOPODA								
Articulata								
Articulata spA	0.1298 ± 0.0189	47 (45.19)	0.1939	0.4169	0.2209	0.1944	0.0422	
Articulata spB	0.0168 ± 0.0084	4 (3.85)		0.0136		0.0416		
Articulata spC	<0.0001	1 (0.96)			0.0042			
Notosaria nigricans pyxidata	0.04 ± 0.008	25 (24.04)	0.3051	0.1476	0.2315			
ARTHROPODA								
Amphipoda	0.0007 ± 0.0001	38 (36.54)						
Epimeria spA	0.0003 ± 0.0001	9 (8.65)			0.0234	0.0098	0.0155	
Themisto gaudicaudii	0.0011 ± 0.0003	14 (13.46)			0.0719	0.0501	0.0026	0.0118
Amphipoda spp.	0.0007 ± 0.0001	38 (36.54)	0.1766	0.0083	0.0469	0.0898	0.026	0.0084
Cirripedia								
Litoscalpellum fissicarinatum	0.0037 ± 0.0006	43 (41.35)	0.0564	0.0498	0.1168	0.0637	0.0851	0.007
Bathylasma corolliforme	0.2923 ± 0.0534	30 (28.85)	0.2143	0.1833	0.0671	0.4377	0.0434	
Cumacea								
Cumacea spA	0.0001	8 (7.69)			0.019	0.0097	0.0052	
Decapoda								
Pasiphaea sp1	0.0037 ± 0.0037	1 (0.96)						0.0273
Thymopides grobovi	0.0093 ± 0.0031	9 (8.65)			0.0138		0.0166	0.168
Isopoda								
Ananthura elegans	0.0003 ± 0.0001	17 (16.35)			0.0287	0.0081	0.0032	
Antarctiuridae sp1	<0.0001	4 (3.85)			0.003			
Antarcturidae sp2	<0.0001	2 (1.92)	0.0794	0.0071	0.0291	0.027	0.0061	
Antarcturus oryx	0.006 ± 0.0008	52 (50)		0.0033	0.0033		0.0051	
Arcturides cornutus	0.001 ± 0.0002	38 (36.54)		0.0036	0.0041			
Asellota sp1	0.0001 ± 0.0001	2 (1.92)	0.3088	0.0973	0.0403	0.1093	0.137	0.0185
Ceratoserolis cornuta	0.0286 ± 0.0051	31 (29.81)	0.1159	0.0169	0.0092	0.0538	0.0958	
Cymodopsis spA	0.0002	22 (21.15)			0.0038		0.0031	
Dolichiscus anna	0.0001 ± 0.0001	3 (2.88)	0.0515	0.0326	0.0814	0.0268	0.1248	0.0684
Euneognathia gigas	0.0008 ± 0.0003	9 (8.65)	0.0198	0.0077	0.0334	0.0296	0.0223	
Isopoda spR	0.0002 ± 0.0001	2 (1.92)				0.0032	0.0065	
Litarcturus granulosus	0.0002 ± 0.0002	1 (0.96)	0.0392	0.0155	0.005	0.0047	0.0099	
Litarcturus stebbingi	0.0003 ± 0.0003	1 (0.96)				0.005	0.0038	
Natatolana intermedia	0.0044 ± 0.002	5 (4.81)					0.0034	
Natatolana oculata	0.0004 ± 0.0002	6 (5.77)					0.0038	
Neastacilla kerguelensis	0.0001	12 (11.54)			0.0055		0.0254	
Serolis gracilis	0.0019 ± 0.0005	14 (13.46)		0.0052	0.0142		0.0092	
Serolis sp.nov.	<0.0001	1 (0.96)		0.0035	0.0081	0.0162	0.0146	
Tuberarcturus spA	0.0001	4 (3.85)	0.0351		0.0099	0.0059	0.0536	0.0126
Ostracoda								
Ostracoda spA	<0.0001	10 (9.62)			0.0046			
Pycnogonida								
Ammothea adunca	0.0048 (0.0022)	5 (4.81)		<0.0001		0.0006	0.0003	
Ammothea sp1*	0.0015 (0.0009)	3 (2.88)					0.0001	
Ammothea sp3	0.0001 (0.0001)	1 (0.96)					<0.0001	
Austropallene sp1	<0.0001	1 (0.96)		<0.0001				

			ASSEMBLAGE					
Taxa	**Biomass**	**Presence**	1	2	3	4	5	6
Austropallene spp.	0.0002 (0.0001)	3 (2.88)				<0.0001	<0.0001	
Colossendeis enigmatica	0.0008 (0.0006)	2 (1.92)		<0.0001	<0.0001			
Colossendeis lilliei	0.0239 (0.012)	4 (3.85)		0.0001		<0.0001	<0.0001	
Colossendeis sp1	0.0023 (0.0008)	9 (8.65)			<0.0001	0.0002	0.0004	
Colossendeis sp2*	0.0002 (0.0001)	3 (2.88)		<0.0001	<0.0001			
Colossendeis spp.	0.0027 (0.0008)	11 (10.58)		<0.0001	<0.0001	0.0016	0.0001	
Decolopoda australis	0.0017 (0.0007)	6 (5.77)			0.0001		0.0002	
Nymphon brachyrhynchum	0.0001 (0.0001)	2 (1.92)					<0.0001	
Nymphon sp1*	0.0002 (0.0001)	8 (7.69)	0.0001	<0.0001	<0.0001		<0.0001	
Nymphon sp3*	<0.0001	2 (1.92)		<0.0001	<0.0001			
Nymphon sp4*	<0.0001	1 (0.96)					<0.0001	
Pallenopsis vanhoffeni	<0.0001	1 (0.96)			<0.0001			
Pseudopallene glutus	<0.0001	1 (0.96)		<0.0001				
Pycnogonum gaini	0.0004 (0.0001)	15 (14.42)			<0.0001			
Pycnogonum sp1*	0.0006 (0.0006)	1 (0.96)	0.0002	<0.0001		<0.0001		
Pycnogonum sp2	0.0006 (0.0003)	4 (3.85)					<0.0001	
Pycnogonid spp.	0.0001 (0.0001)	1 (0.96)	<0.0001		<0.0001	0.0001	<0.0001	<0.0001
Tanaidacea								
Apseudomorpha spA	<0.0001	3 (2.88)		0.0122		0.0586	0.0063	
Nototanais spA	0.0035 ± 0.0006	34 (32.69)		0.0057	0.012			
Tanaidacea spA	<0.0001	4 (3.85)			0.0123			
ECHINODERMATA								
Asteroidea								
Acodontaster elongatus	0.0428 ± 0.0082	27 (25.96)	0.1243	0.0422	0.0583	0.0128	0.0673	
Anteliaster australis	0.0007 ± 0.0007	1 (0.96)					0.0061	
Asteriidae spA	0.5721 ± 0.1011	32 (30.77)	0.2599	0.1828	0.1811	0.0686	0.0185	
Asteroidea spA	0.0015 ± 0.001	2 (1.92)		0.008				
Asteroidea spC	0.0001 ± 0.0001	2 (1.92)	0.6127	0.0983	0.1998	0.0552	0.2465	
Asteroidea spD	0.0001 ± 0.0001	2 (1.92)			0.0039		0.0066	
Asteroidea spE	<0.0001	1 (0.96)			0.0046	0.0072		
Asteroidea spG	0.005 ± 0.002	6 (5.77)			0.0106			
Bathybiaster loripes	0.2638 ± 0.033	64 (61.54)			0.0047			
Brisingida spA	0.0561 ± 0.0561	1 (0.96)				0.0599	0.0156	
Cheiraster (Luidiaster) *hirsutus*	0.0543 ± 0.0099	30 (28.85)		0.1605	0.2566	0.048	0.6368	0.1786
Crossaster cf. *penicillatus*	0.2567 ± 0.1815	2 (1.92)				0.0324		
Crossaster spA	0.1233 ± 0.1233	1 (0.96)	0.0504	0.03	0.0911	0.0215	0.2635	
Cuenotaster involutus	0.0326 ± 0.0069	22 (21.15)				0.0441	0.0215	
Cycethra verrucosa	0.0793 ± 0.03	7 (6.73)				0.0395		
Diplasterias meridionalis	0.0129 ± 0.0028	21 (20.19)	0.0465	0.1515	0.0965	0.1531	0.0041	
Henricia obesa	0.1983 ± 0.1983	1 (0.96)	0.2563	0.0413	0.0253			
Henricia spA	0.0052 ± 0.0012	18 (17.31)	0.0795	0.0469	0.1238	0.0131	0.0496	
Hippasteria falklandica	0.5741 ± 0.0999	33 (31.73)	0.0953					
Hymenaster spA	0.0011 ± 0.0002	27 (25.96)	0.0462	0.1064	0.0492	0.0316	0.0191	
Labidiaster annulatus	0.1377 ± 0.0189	53 (50.96)	0.6595	0.1431	0.3759	0.4776	0.0547	
Leptychaster kerguelensis	0.0634 ± 0.0116	30 (28.85)	0.0739	0.0232	0.0734	0.0419	0.0368	
Leptychaster spA	0.0187 ± 0.0041	21 (20.19)	0.4141	0.1198	0.1737	0.3785	0.3083	
Lophaster spA	0.0018 ± 0.0013	2 (1.92)		0.052	0.092	0.0706	0.1747	
Odontaster meridionalis	0.0209 ± 0.0034	37 (35.58)	0.1327	0.084	0.0723	0.12	0.0263	
Porania antarctica	0.0235 ± 0.0046	26 (25)				0.0254		
Porcellanasteridae spA	0.0027 ± 0.0019	2 (1.92)	0.2222	0.1883	0.1074	0.1139	0.0609	
Pseudarchaster spA	0.0287 ± 0.0166	3 (2.88)	0.2585	0.1382	0.0885	0.0373	0.059	
Pteraster rugatus	0.0125 ± 0.0022	31 (29.81)	0.0385		0.0047			
Pteraster spA	0.0173 ± 0.0035	25 (24.04)		0.0102	0.0156		0.0151	
Pteraster spB	0.3038 ± 0.0555	30 (28.85)	0.1141	0.1697	0.1868	0.0307	0.0108	
Pteraster spC	0.0185 ± 0.0049	14 (13.46)	0.0897	0.1495	0.0902	0.0657	0.0339	
Rhopiella hirsuta	0.0269 ± 0.011	6 (5.77)	0.5798	0.1812	0.2491	0.1844	0.0115	0.1563
Smilasterias triremis	0.1006 ± 0.0124	66 (63.46)	0.1448	0.0896	0.0359	0.0538		
Solaster regularis subarcuatus	0.1232 ± 0.0299	17 (16.35)	0.0854	0.0161		0.0201	0.0187	

			ASSEMBLAGE					
Taxa	**Biomass**	**Presence**	1	2	3	4	5	6
Tremaster mirabilis	0.1885 ± 0.0356	28 (26.92)	0.8061	0.3756	0.2317	0.2938	0.1056	
Crinoidea								
Promachocrinus kerguelensis	0.1484 ± 0.0332	20 (19.23)	0.1309	0.2197	0.0291	0.1463		
Solanometra antarctica	0.0573 ± 0.0073	62 (59.62)		0.3998	0.2852	0.1955		
Echinoidea								
Abatus cordatus	0.0107 ± 0.0076	2 (1.92)	0.2974	0.148	0.1444	0.0509		
Brisaster antarcticus	0.7901 ± 0.1117	50 (48.08)	0.3947	0.2068	0.3593	0.2271	0.1193	0.0251
Dermechinus horridus	0.0293 ± 0.0293	1 (0.96)	0.0474				0.0089	
Sterechinus diadema	0.133 ± 0.016	69 (66.35)	0.0329	0.0312	0.0789	0.0455	0.5878	0.0936
Ctenocidaris nutrix	0.1331 ± 0.0168	63 (60.58)		0.0207				
Euryalida								
Asteronyx loveni	0.3508 ± 0.0688	26 (25)	0.9214	0.3442	0.3561	0.3705	0.1608	
Astrotoma agassizii	0.0708 ± 0.0236	9 (8.65)	0.7901	0.4543	0.4095	0.2662	0.0694	
Gorgoncephalus chilensis	0.1126 ± 0.0252	20 (19.23)	0.0756	0.0142	0.1356	0.0599	0.1603	0.3174
Holothuroidea								
Cucumaria kerguelensis	0.0012 ± 0.0007	3 (2.88)			0.0243	0.1265	0.0438	
Cucumariidae sp1*	0.0002 ± 0.0002	1 (0.96)		0.0875	0.1178	0.1494	0.0875	
Dactylochirotida sp.nov.*	0.0869 ± 0.0355	6 (5.77)	0.0348	0.0035	0.0044			
Heterocucumis godeffroyi	0.0019 ± 0.0007	7 (6.73)			0.0062			
Molpadia musculus	0.1901 ± 0.085	5 (4.81)			0.0093		0.0491	0.0756
Molpadiidae sp.nov.*	0.0172 ± 0.007	6 (5.77)		0.0381	0.0242			
Pseudocnus laevigatus	0.0313 ± 0.0038	67 (64.42)	0.1126	0.0252	0.0148		0.0343	
Pseudocnus serrata	<0.0001	2 (1.92)			0.0104		0.0181	0.1249
Pseudostichopus cf. *peripatus* (a)	0.002 ± 0.001	4 (3.85)	0.6481	0.1409	0.1737	0.1486	0.1015	
Pseudostichopus cf. *peripatus* (b)	0.0039 ± 0.0018	5 (4.81)			0.0084			
Pseudostichopus peripatus	0.0011 ± 0.0003	12 (11.54)			0.0319	0.014		
Pseudostichopus sp.nov.*	0.0084 ± 0.0049	3 (2.88)			0.0117		0.0265	
Pseudostichopus sp1	0.0006 ± 0.0006	1 (0.96)		0.0439	0.0611			
Psolidium poriferum	0.0073 ± 0.0015	24 (23.08)			0.046			
Psolus ephippifer	0.0029 ± 0.0008	13 (12.5)					0.0045	
Psolus paradubiosus	0.124 ± 0.0187	44 (42.31)	0.1841	0.0361	0.0438	0.0851	0.0204	
Psolus sp.nov. *	0.0001	3 (2.88)	0.0706	0.0509	0.0295	0.0125	0.0029	
Staurocucumis liouvillei	0.646 ± 0.082	62 (59.62)	0.6249	0.2203	0.2363	0.1857	0.0473	
Synallactes sp.nov.*	0.0011 ± 0.0008	2 (1.92)			0.01	0.0053		
Trachythyone muricata	0.0017 ± 0.0005	10 (9.62)	1.3107	0.3426	0.4234	0.148	0.1989	
Ophiuroidea								
Amphiura (Amphiura) cf. *alternans*	0.0116 ± 0.0016	52 (50)			0.012	0.007		
Amphiura (Amphiura) sp2	<0.0001	3 (2.88)			0.0154		0.0328	0.0434
Astrophiura permira	0.0001	3 (2.88)	0.4686	0.1233	0.1066	0.1358	0.0298	
Ophiacamax sp1	0.0277 ± 0.0277	1 (0.96)			0.0033		0.0036	
Ophiacantha imago	0.0016 ± 0.0003	30 (28.85)			0.0092	0.0047		
Ophiacantha pentactis	0.015 ± 0.0026	34 (32.69)						0.0453
Ophiacantha vivipara	0.0336 ± 0.0048	50 (48.08)	0.1303	0.0827	0.0473	0.0281	0.017	
Ophiocten amitinum	0.0012 ± 0.0003	15 (14.42)	0.2708	0.0931	0.0437	0.1992	0.0268	0.1265
Ophiogena laevigata	0.1597 ± 0.0249	41 (39.42)	0.2924	0.1462	0.0897	0.2952	0.095	
Ophiolebella biscutifera	0.0006 ± 0.0001	19 (18.27)		0.0025	0.0098	0.0162	0.0517	
Ophiolimna antarctica	0.0114 ± 0.0034	11 (10.58)		0.0504	0.0666	0.0377	0.4356	0.0721
Ophiomisidium speciosum	0.0001	14 (13.46)	0.0629	0.0185	0.0509	0.0291	0.0075	
Ophiomitrella conferta	0.0001 ± 0.0001	1 (0.96)		0.1504	0.0114			
Ophionotus hexactis	0.2928 ± 0.0655	20 (19.23)	0.0446	0.0047	0.0418	0.0042		
Ophiura sp1	0.0011 ± 0.0011	1 (0.96)			0.005			
Ophiuroglypha ambigua	0.0037 ± 0.0004	67 (64.42)				0.0155	0.293	0.0485
Ophiurolepis carinata	0.1772 ± 0.021	71 (68.27)				0.0122		
Theodoria cf. *relegata*	0.0004 ± 0.0001	8 (7.69)	0.087	0.084	0.1169	0.1012	0.1879	0.0177
HEMICHORDATA								
Pterobranchia								
Pterobranchia spA	0.1154 ± 0.0218	28 (26.92)	0.9844	0.3196	0.4763	0.2804	0.1377	

Taxa	Biomass	Presence	ASSEMBLAGE 1	2	3	4	5	6
Pterobranchia spB	0.0119 ± 0.0036	11 (10.58)	0.0241		0.0111	0.0073	0.0149	
UROCHORDATA								
Ascidiacea								
Ascidia challengeri	0.1714 ± 0.0495	12 (11.54)	0.2952	0.1097	0.1675	0.0351	0.0409	
Ascidia spA	0.2557 ± 0.0852	9 (8.65)	0.0565	0.0158	0.0656	0.0467	0.0121	
Ascidiacea spA	0.0713 ± 0.0356	4 (3.85)		0.2926	0.0126			
Cnemidocarpa verrucosa	0.3875 ± 0.0746	27 (25.96)	0.1587	0.2092				
Molgula pedunculata	0.1848 ± 0.0279	44 (42.31)		0.047	0.0495			
Sycozoa sigillinoides	0.0051 ± 0.0017	9 (8.65)	0.2401	0.3636	0.0869	0.1224	0.0426	
Tylobranchion speciosum	0.0052 ± 0.003	3 (2.88)		0.5827	0.2006	0.1068	0.1788	0.0194
Ascidiacea spp.	0.3236 ± 0.0387	70 (67.31)		0.0133	0.0657	0.0496		

Table 5 Diversity and composition of benthic phyla/subphyla in the HIMI region. Presence = total number (or percentage in paranthese) of station records out of 104. Biomass ($g.m^{-2}$) and abundance ($n.m^{-2}$, non-colonial taxa only) = mean value across all stations ± standard error (SE). Estimates of diversity (taxa) should be considered a minimum estimate, particularly for colonial groups that were generally classified at a low taxonomic resolution.

Phyla/subphyla	Taxa	Presence (%)	Biomass ± SE	Abundance ± SE
Porifera	11	91 (87.5)	6.0807 ± 0.6374	
Cnidaria	57	100 (96.15)	0.3353 ± 0.0335	
Platyhelminthes	2	5 (4.81)	0.0039 ± 0.0017	<0.001 ± <0.001
Brachiopoda	4	51 (49.04)	0.1406 ± 0.0197	0.052 ± 0.013
Priapula	1	3 (2.88)	0.0034 ± 0.002	<0.001 ± <0.001
Sipuncula	6	6 (5.77)	0.0309 ± 0.0126	<0.001 ± <0.001
Bryozoa	1	72 (69.23)	0.9427 ± 0.1111	
Annelida	3	86 (82.69)	1.0247 ± 0.1105	0.041 ± 0.008
Mollusca	80	91 (87.5)	0.1477 ± 0.0155	0.111 ± 0.022
Crustacea	32	98 (94.23)	0.1264 ± 0.0128	0.107 ± 0.027
Pycnogonida	21	55 (52.88)	0.361 ± 0.0005	0.013 ± 0.001
Echinodermata	84	104 (100)	2.388 ± 0.2342	0.592 ± 0.010
Pterobranchia	2	35 (33.65)	0.096 ± 0.0162	
Ascidiacea	8	84 (80.77)	0.547 ± 0.0597	

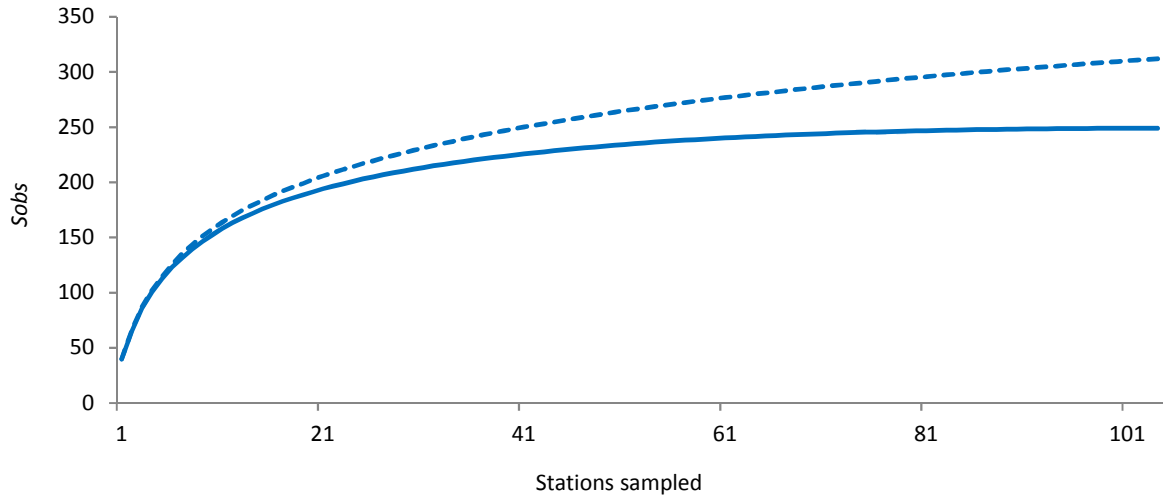

Fig. 7 Species-accumulation plots displaying cumulative species observations (*sobs*) with successive pooling of samples across HIMI. Plots show *sobs* for all 312 taxa (dashed-line) and those 249 remaining after removal of station-restricted taxa (i.e. taxa recorded from only one station) (solid-line).

1.4.2 Assemblage distribution and structure

Across all stations and taxa a total of 30,888 records of biomass were made, all of which were included in subsequent analyses of community structure and function. PAM clustering of biomass data indicated that $k = 2$ (k_2) provided the best data partition, achieving maximum CH_k (15.67). CH_k was also high for the 6-group solution (k_6) (CH_k = 13.38) (Table 6). Analysis of the k_2 and k_6 solutions using the ANOSIM test statistic revealed a higher value of R for k_6 (ANOSIM R = 0.54 k_2 and 0.65 k_6). In addition, k_6 provided a better representation of the stations in 2-dimensions with the exception of some station overlap (Fig. 8). Thus, k_6 (with stations ranked from Assemblage 1 – Assemblage 6, where 1 = highest biomass and 6 = lowest biomass) was selected as the most appropriate partitioning of the HIMI data and was used in subsequent analyses and plots.

Table 6 Values of the Calinski-Harabasz criterion (CH_k) calculated on the basis of Bray-Curtis similarities of transformed taxa biomass data ($g.m^{-2}$) for each of PAM $k = 2, 3, \ldots, 10$ groups solutions.

PAM groups (k)	CH_k
k_2	**15.670**
k_3	10.614
k_4	9.316
k_5	8.270
k_6	**13.381**
k_7	10.284
k_8	8.930
k_9	8.372
k_{10}	8.609

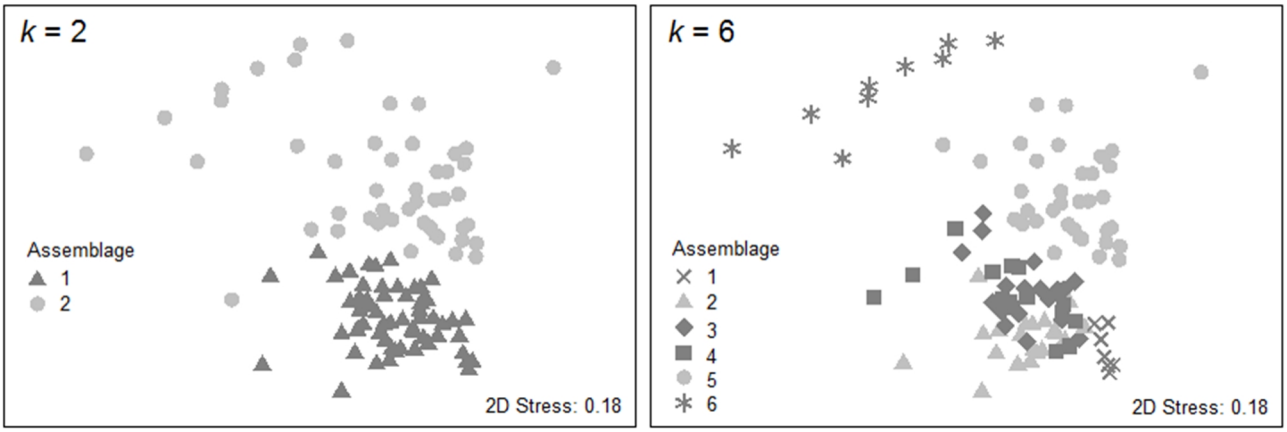

Fig. 8 Non-metric MDS ordinations of stations according Bray-Curtis dissimilarities calculated on transformed taxa biomass data ($g.m^{-2}$). In each ordination stations are colour coded according to their PAM ***k*** 2-group and 6-group solutions.

The distribution of the six distinct faunal assemblages was tightly linked with sampling area and geomorphology, i.e. bank, plateau or slope. Assemblage 1 consisted of six stations in predominantly shallow waters at PBA (<300 m depth) and one on the upper margin of SSW the shallowest station sampled in this study at 168 m depth (Fig. 9, Table 7). Assemblage 2 included the majority of stations from the western banks including CBA and ABA, while Assemblage 3 consisted largely of stations on the top of SBA. Assemblage 4 was the dominant assemblage at SSW stations, whilst Assemblage 5 included the majority of stations from neighbouring SSE, and the plateau seascapes of GRI and WPL. Finally, Assemblage 6 included nine stations in deep water across NEP and at the base of SBA (mostly > 700 m depth).

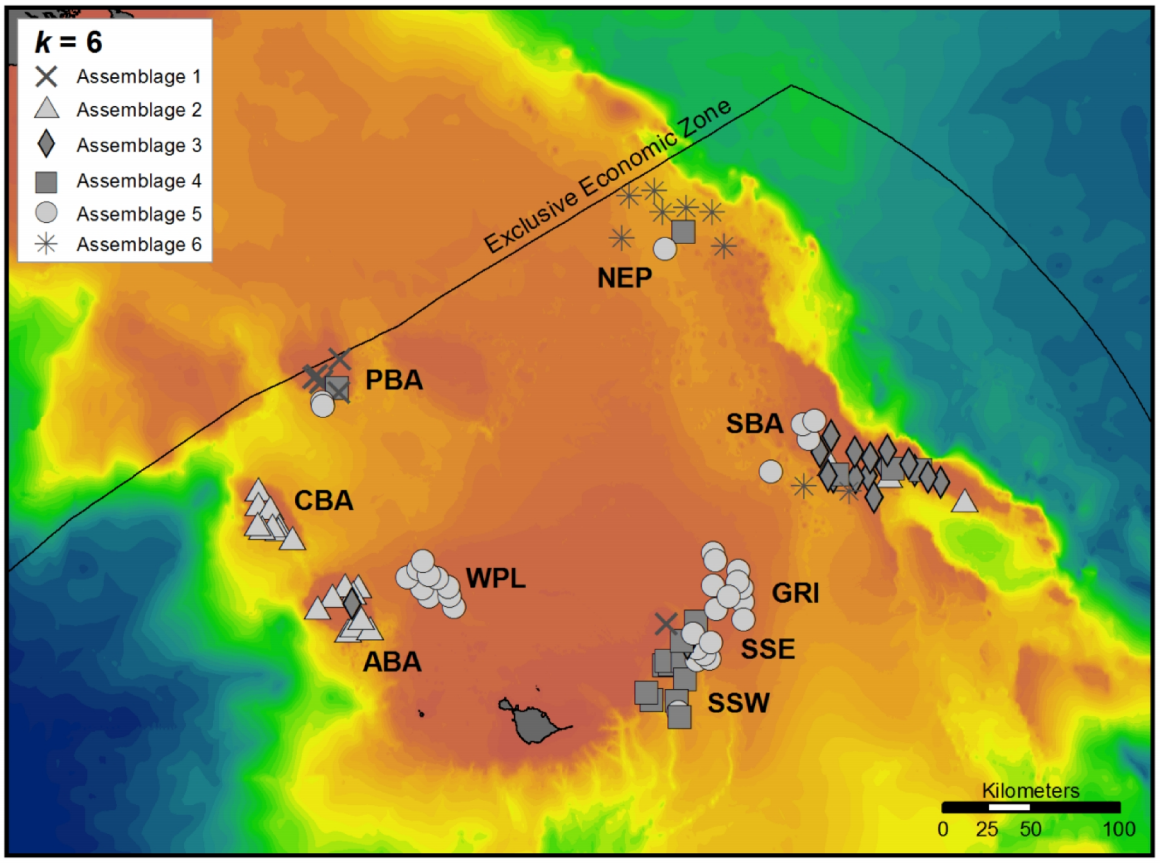

Fig. 9 Sampling stations across HIMI colour-coded according to their PAM *k* 6-group solution.

Table 7 Characteristics of the 6 assemblages identified via PAM clustering. Data includes the total number of stations characterised by each assemblage and their respective mean for depth (m), biomass ($g.m^{-2}$), species richness (*S*) and fishing disturbance (km^2). The range of values across stations (min – max) is also presented.

Assemblage	**1**	**2**	**3**	**4**	**5**	**6**
Stations	7	20	18	15	35	9
Depth	288.71 (168-496)	309.65 (222-445)	298.06 (212-557)	513.33 (256-941)	405.11 (218-820)	777.33 (472-970)
Biomass	103.02 (24.12-181.64)	4.69 (0.23-18.92)	3.95 (0.22-31.81)	3.19 (0.05-11.93)	3.96 (0.01-24.09)	0.13 (0.003-0.42)
Richness	44.43 (37-54)	43.45 (14-75)	49.06 (22-79)	41.47 (13-66)	37.77 (6-68)	8 (2-11)
Disturbance	0.52 (0.23-1.68)	0.33 (0-1.05)	0.38 (0-2.25)	0.66 (0-2.6)	0.28 (0-1.13)	0.15 (0-0.73)

The biomass proportion of sessile suspension-feeding taxa versus mobile predators and/or detritivores was key to differentiating these six assemblages (Fig. 10, Table 8). Biomass was particularly high for stations that were characterised by Assemblage 1 (Table 7) due to high densities of sessile taxa (Fig. 10), namely poriferans (Demospongiae and Hexactinelidae), bryozoans, serpulid tube worms and ascidians (Table 8). Sessile fauna were also the most dominant at stations that were characterised by Assemblages 2 and 3 (Fig. 10), including poriferans in Assemblage 2, bryozoans and serpulids in Assemblage 3, and ascidians in both (Table 8). Asteroids and echinoids were also important in both assemblages; although all groups were lower in biomass than Assemblage 1 (Table 8). Cirripeds were highly abundant at stations that were characterised by Assemblage 4, and other sessile suspension-feeders (including serpulids and ascidians) were also important by weight being present at biomasses similar to Assemblages 2 and 3 (Table 8). Stations that were characterised by Assemblage 5 were dominated by polychaetes, echinoids and actinarians (Table 8), with a higher proportion of mobile predators and detritivores than Assemblages 2, 3 and 4 (Fig. 10). Stations characterised by Assemblage 6 had low biomass (Table 7), and were not dominated by any single group (Fig. 10, Table 8).

Species richness was highest for Assemblage 3 despite a lower biomass than Assemblage 1 (Table 7). Assemblages 1, 2 and 4 were characterized by an intermediate to high species richness, while Assemblage 6 was particularly depauperate. The range of species richness values for each of the assemblages was high, suggesting that each was characterised by a discrete set of dominant taxa. For Assemblage 1, these dominant taxa, as identified by SIMPER, included *Serpula* spA (Polychaete) and the echinoderms *Smilasterias triremis*, *Sterechinus diadema*, *Staurocucumis liouvillei* and *Ophiurolepis carinata* (Table 8). Interestingly, *Bathybiaster loripes,* one of the most common asteroids across the HIMI region, was absent from this assemblage. Species typifying Assemblage 2

were the demosponge *Tetilla leptoderma*, Hexactinellida spA and the asteroid *Tremaster mirabilis*; while *O. carinata* (Ophuiroidea), *Solanometra antarctica* (Crinoidea) and *Aphroditidae* spA (Polychaete) were key to Assemblage 3. The cirriped *Bathylasma corolliforme* was particularly common in Assemblage 4, as were the asteroids *Hippassteria falklandica* and *Labidiaster annulatus*. Key taxa to Assemblage 5 were *Aphroditidae* spA, *Liponema* spA (Actinaria), *Flabellum* spA (Scleractinia), *Dentalium aegum* (Mollusca), plus a number of echinoderms. Finally, for Assemblage 6, the Bellator lobster *Thymopides grobovi* and euryalid *Asteronyx loveni* were key to the overall faunal composition for stations characterized by this assemblage.

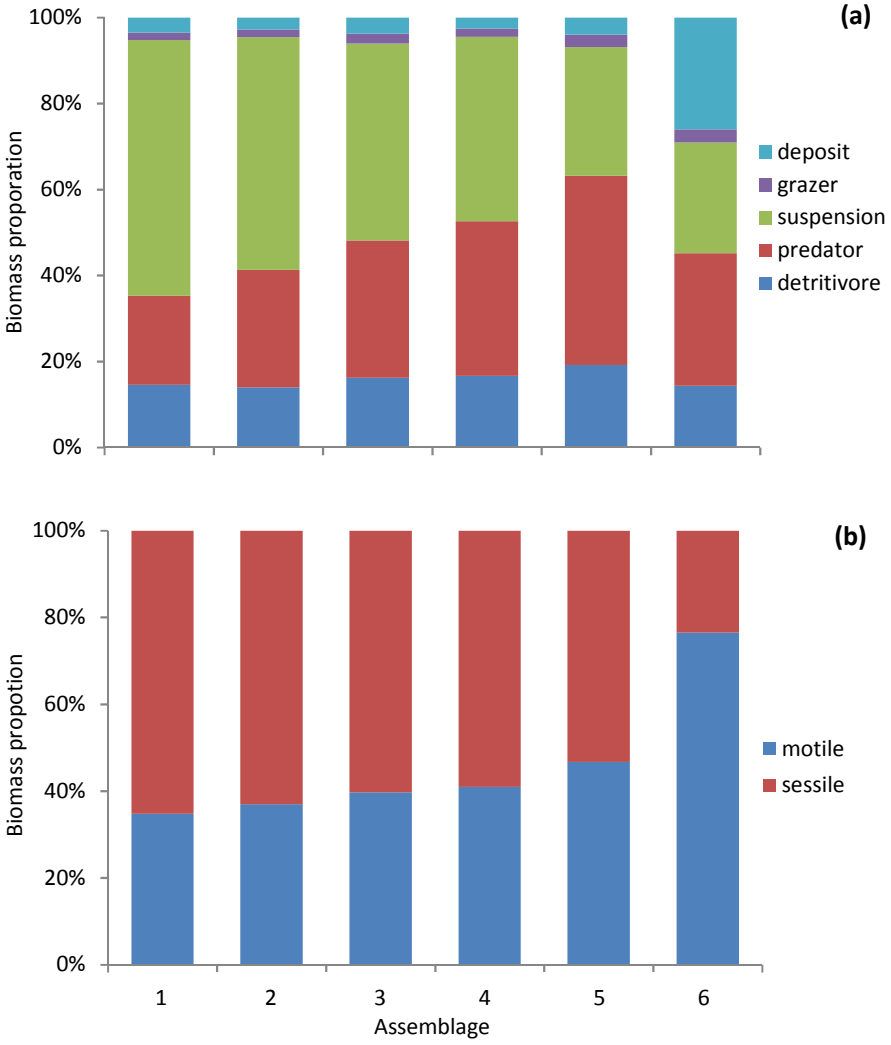

Fig. 10 **(a)** Feeding structure of the 6 assemblages throughout the HIMI region. Each bar represents the average biomass ($g.m^{-2}$) of that assemblage, divided into 5 feeding guilds (detritivore), predator, suspension-feeder, grazer or deposit-feeder. For example, Assemblage 1 was characterised by a biomass of ~30 $g.m^{-2}$ of which more than half were suspension-feeders. Error bars denote standard errors. **(b)** Motility structure, i.e. the biomass proportion (%) of motile versus sessile taxa at stations characterised by each assemblage.

Table 8 Differences in faunal composition between assemblages and specific discriminator taxa detected by SIMPER (cells shaded grey). Discriminator taxa were defined as those contributing >5% to among group dissimilarity and with a high dissimilarity to standard deviation ratio (Diss/SD > 1.5). Values are transformed biomass ($g.m^{-2}$).

Assemblage	1	2	3	4	5	6
CLASS/ORDER						
Demospongiae	0.484	0.278	0.137	0.116	0.084	0.001
Hexactinellida	0.725	0.289	0.166	0.029	0.008	
Actinaria	0.017	0.024	0.019	0.023	0.084	0.005
Bryozoa	1.53	0.154	0.467	0.369	0.205	0.034
Polychaeta	0.283	0.026	0.082	0.095	0.316	0.044
Serpulidae	1.493	0.124	0.297	0.245	0.206	0.013
Bivalvia	0.048	0.01	0.013	0.008	0.015	
Gastropoda	0.011	0.005	0.011	0.008	0.028	
Cirripedia	0.107	0.092	0.034	0.219	0.022	
Asteroidea	0.165	0.103	0.102	0.089	0.071	0.011
Ophiuroidea	0.148	0.067	0.068	0.073	0.081	0.017
Holothuroidea	0.166	0.05	0.065	0.034	0.03	0.014
Echinoidea	0.448	0.207	0.211	0.171	0.207	0.023
Ascidiacea	1.27	0.534	0.449	0.493	0.157	0.003
TAXA						
Tetilla leptoderma (Demospongiae)	0.554	0.749	0.194		0.07	
Hexactinellida spA (Hexactinellida)		0.384	0.284		0.009	
Liponema spA (Scleractinia)		0.063	0.014	0.077	0.304	
Flabellum spA (Scleractinia)		0.01	0.05	0.039	0.163	0.024
Aphroditidae spA (Polychaete)	0.069	0.043	0.11	0.045	0.473	
Serpula spA (Polychaete)	1.493	0.124	0.297	0.245	0.206	0.013
Articulata spA (Brachipoda)	0.194	0.417	0.221	0.194	0.042	
Notosaria nigricans pyxidata (Brachipoda)	0.305	0.148	0.231			
Dentalium aegeum (Mollusca)	0.049		0.028		0.142	
Bathylasma corolliforme (Cirripedia)	0.214	0.183	0.067	0.438	0.043	
Thymopides grobovi (Decapoda)			0.014		0.017	0.168
Smilasterias triremis (Asteroidea)	0.806	0.376	0.232	0.294	0.106	
Hippasteria falklandica (Asteroidea)	0.66	0.143	0.376	0.478	0.055	
Labidiaster annulatus (Asteroidea)	0.414	0.12	0.174	0.379	0.308	
Pteraster spB (Asteroidea)	0.58	0.181	0.249	0.184	0.011	0.156
Bathybiaster loripes (Asteroidea)		0.161	0.257	0.048	0.637	0.179
Asteriidae spA (Asteroidea)	0.613	0.098	0.2	0.055	0.246	
Tremaster mirabilis (Asteroidea)		0.4	0.285	0.195		
Cheiraster (Luidiaster hirsutus (Asteroidea)	0.05	0.03	0.091	0.022	0.264	
Solanometra Antarctica (Crinoidea)	0.395	0.207	0.359	0.227	0.119	0.025
Sterechinus diadema (Echinoidea)	0.921	0.344	0.356	0.371	0.161	
Ctenocidaris nutrix (Echinoidea)	0.79	0.454	0.41	0.266	0.069	
Brisaster antarcticus (Echinoidea)	0.033	0.031	0.079	0.045	0.588	0.094
Asteronyx loveni (Euraylida)	0.076	0.014	0.136	0.06	0.16	0.317
Staurocucumis liouvillei (Holothuroidea)	1.311	0.343	0.423	0.148	0.199	
Psolus paradubiosus (Holothuroidea)	0.625	0.22	0.236	0.186	0.047	
Pseudocnus laevigatus (Holothuroidea)	0.648	0.141	0.174	0.149	0.101	
Ophiurolepis carinata (Ophuiroidea)	0.984	0.32	0.476	0.28	0.138	
Ophiacantha vivipara (Ophuiroidea)	0.292	0.146	0.09	0.295	0.095	
Ophiacantha pentactis (Ophuiroidea	0.271	0.093	0.044	0.199	0.027	0.127
Ophiogena laevigata (Ophuiroidea)		0.05	0.067	0.038	0.436	0.072
Ophionotus hexactis (Ophuiroidea)				0.016	0.293	0.049
Molgula pedunculata (Ascidiacea)		0.583	0.201	0.107	0.179	0.019

1.4.3 Links between environmental variables and the distribution of faunal assemblages

A combination of ten environmental variables explained 39.53% of the variance in the taxa biomass data (Table 9). Individually, the single variable that explained the greatest amount of variation was the contrast between high and low seafloor current speeds (i.e. *btm.spd*, 8.25%), followed closely by changes in water depth (i.e. *depth*, 7.48%). Sequentially, seafloor current speed, seafloor temperature (*btm.tmp*), particulate organic carbon (*poc*) and water depth were fundamental to explaining community variance across HIMI. Stations that were characterised by Assemblages 1, 2, 3 and 4 were generally shallower and had higher current speeds than stations that were characterised by Assemblage 6 (Fig. 11). Stations that were characterised by Assemblage 5 generally had a higher concentration of particulate organic carbon and nitrate (*btm.nit*) than stations that were characterised by Assemblage 6 which were further differentiated by warmer seafloor temperatures and a large separation distance from the shelf break (*dist.shf*). The fact that the constrained dbRDA ordination showed similar patterns to the unconstrained MDS plot (Fig. 8) suggests that differences in assemblages were well identified by the suite of predictor variables modelled.

Table 9 distLM results of multivariate taxa biomass data against ten predictor variables selected for inclusion in the model. Results are presented for **(a)** each variable individually (marginal tests) and then **(b)** fitted sequentially using step-wise forward-selection of variables. Variables are arranged according to Cum. %: cumulative percentage of variance explained. %Var: percentage of the variance in the taxa data explained by that variable.

	(a) Marginal tests			**(b) Forward selection sequential tests**			
Variable	*Pseudo-F*	*P*	*% Var*	*Pseudo-F*	*P*	*% Var*	*Cum. %*
Seafloor current speed (btm.spd)	9.175	>0.001	8.25	9.175	>0.001	8.25	8.25
Temperature (btm.tmp)	6.627	>0.001	6.1	7.357	>0.001	6.23	14.48
Particulate organic carbon (poc)	6.637	>0.001	6.11	7.720	>0.001	6.13	20.61
Depth	8.241	>0.001	7.48	6.845	>0.001	5.13	25.74
Dissolved oxygen (btm.oxy)	3.635	>0.001	3.44	4.656	>0.001	3.37	29.11
Nitrate (btm.nit)	3.844	>0.001	3.63	4.971	>0.001	3.46	32.57
Silicate (btm.sil)	4.724	>0.001	4.43	3.658	>0.001	2.47	35.04
Distance to shelf break (dist.shf)	6.561	>0.001	6.04	2.520	>0.001	1.68	36.72
Distance to sub-Antarctic island (dist.isl)	6.150	>0.001	5.99	2.139	0.002	1.42	38.14
Seafloor vertical velocity (btm.vvl)	5.694	>0.001	5.69	1.672	0.019	1.07	39.53

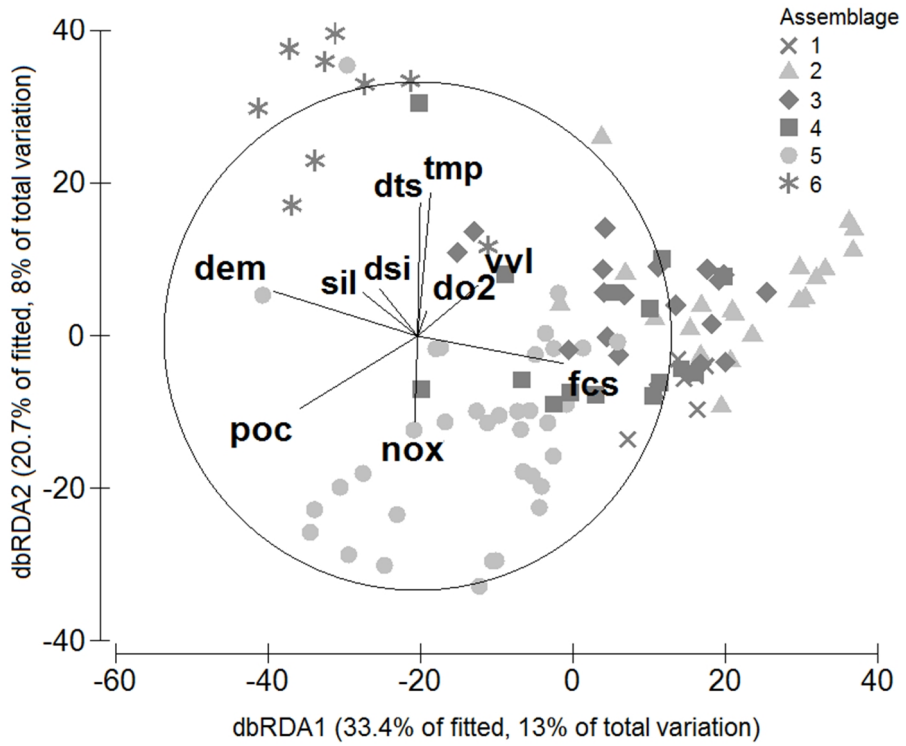

Fig. 11 Results from a dbRDA ordination relating benthic sampling stations and their assemblage classification to environmental variables throughout HIMI. The vector plot overlaid shows the 10 most important variables as determined by forward selection distLM. The length of the vector is representative of the strength of the correlation between the variable and either of the dbRDA axes (dbRDA1 and dbRDA2). For example, seafloor current speed (*fcs*) was strongly positively correlated to dbRDA1, while *poc* is negatively correlated to that axis. Other variables include temperature (*tmp*), particulate organic carbon (*poc*), depth (*dem*), dissolved oxygen (*do2*), nitrate (*nox*), silicate (*sil*), distance to shelf break (*dts*), distance to sub-Antarctic island (*dsi*) and seafloor vertical velocity (*vvl*).

1.5 Discussion

1.5.1 Biodiversity in a regional context

The benthic communities of HIMI were diverse and represent a unique sub-Antarctic marine fauna that is worthy of conservation. Across the localities sampled I identified 312 taxa from 13 phyla, of which 14 taxa were undescribed and likely to be endemic. This represents a dramatic increase in the diversity previously catalogued for the HIMI region (Meyer *et al.* 2000), and indicates important conservation values exist in the area.

Like many cold temperate, sub-Antarctic and Antarctic areas, the shallower shelf depths at HIMI (≤400 m) were dominated by sessile suspension-feeding benthos. Some taxa were very diverse or represented by a large biomass, like poriferans, cnidarians, bryozoans and ascidians. Below these depths, echinoderms and pycnogonids dominated, with many species ubiquitous across HIMI. A dominance of sessile suspension-feeders in shallower water, and a high diversity and abundance of echinoderms and pycnogonids, was also noted for the neighbouring French territory of Isles Kerguelen on the Northern Kerguelen Plateau (Améziane *et al.* 2011).

The benthic diversity and richness at HIMI was intermediate relative to shelf communities elsewhere. Richer areas have been sampled, for example, on the continental shelf of Antarctica (Gutt & Starmans 1998) and Australia (Williams *et al.* 2010). Diversity and richness was instead comparable to high latitude islands in the sub-Antarctic and South Atlantic, including Prince Edward (Branch *et al.* 1993) and Bouvet (Gutt *et al.* 2006), which like HIMI, are isolated from continental influences. However, a conclusion about the relative diversity of benthos at HIMI compared with these communities elsewhere is hampered by inconsistent sampling methods (i.e. gear type or mesh diameter) and taxonomy (e.g. unclassified groups). Phyla like Porifera and Bryozoa, which are largely unclassified for HIMI, may yield some of the highest species numbers of all groups. Améziane *et al.* (2011) identified 111 poriferans from the Isles Kerguelen region, and the diversity of this group at shelf depths elsewhere is typically high (e.g. Gray 2001, Clarke & Johnstone 2003, Arntz *et al.* 2006). In addition, many habitats and taxa were not sampled in this study. For instance, the area inside the 12 nm territorial sea around Heard Island was not sampled in this study, and yet previous research (albeit mostly qualitative) has suggested that this area hosts a different suite of taxa compared with deeper waters offshore (Meyer *et al.* 2000). Further scrutiny of unclassified groups and sampling of the territorial sea would undoubtedly add further species to the HIMI list. In addition, the recorded biodiversity presented in this study is likely to be an underestimate as infauna and taxa smaller than the mesh size used would have been poorly sampled.

I cannot comment conclusively on the proportion of endemics at HIMI, particularly as knowledge of Southern Ocean biodiversity is largely incomplete. Only holothurians and pycnogonids were scrutinised by expert taxonomists and both groups had high levels of undescribed and endemic species. Similarly the majority of bivalve and gastropod molluscs identified thus far are thought to be undescribed (E. Turner, personal communication, January 30, 2012), suggesting high levels of endemism.

Sub-Antarctic islands are considered likely to have low diversity and high degrees of endemism due to their isolation, unique oceanographic influences and small size (Branch *et al.* 1993, Gutt *et al.* 2006). The intermediate diversity and high numbers of undescribed species observed here (despite some groups being incompletely sorted) tend to support this claim. HIMI and Isles Kerguelen are more than 1500 kilometres from any equivalent habitats, i.e. seascapes less than 1000 m depth. They do however lie directly in the path of the ACC, the dominant circulation feature of the Southern Ocean, and a mode of dispersal for benthic fauna. When Antarctica separated from Gondwana some 14 million years ago, the ACC established a strong flow of water from west to east, effectively isolating the Antarctic continent and much of the sub-Antarctic region from more northern influences. The ACC has since had attributed to it a major role in the diversification of benthic habitats of the Southern Ocean (Arntz *et al.* 1997, Saucède *et al.* 2014a). Depending on the taxa (broadcasters versus brooders), the ACC has promoted either allopatric speciation and diversification (Pearse *et al.* 2009) or long-distance connectivity between populations (Janosik *et al.* 2011) or closely related species (Barnes & Griffiths 2008, Waters 2008, Leese *et al.* 2010) in many invertebrates (eg. echinoderms, bryozoans, crustaceans). For instance, studies on Bouvet Island benthos found faunal affinities with the Antarctic Peninsula, near the Antarctic continent and the Magellanic region of South America (Arntz *et al.* 2006); connectivity partially attributed to the ACC. Similarly, Butler *et al.* (2000a) found few species with restricted distributions around Macquarie Island, and instead described the island as a biogeographic contact zone with mixing of many species from surrounding waters brought to the island via prevailing currents. Conversely, the AAC has been attributed particularly high levels of endemicity in the Southern Ocean due to the barrier-effect its strong east-ward flow has on latitudinal dispersal (i.e. between Antarctic, sub-Antarctic and temperate waters) (Pearse *et al.* 2009). Within the HIMI region itself, the presence of a typical high latitude benthic assemblage dominated by slow growing, sessile suspension-feeders and echinoderms, and the presence of many potential circumpolar taxa like *Notocidaris mortenseni* (Saucède *et al.* 2014b), *Ctenocidaris nutrix* (Kroh 2013), *Bathybiaster loripes* (Mah 2013), *Staurocucumis liouvillei* (Paulay & Bohn 2013), would suggest faunal affinities between HIMI, the

Antarctic and other sub-Antarctic islands. However, intermediate-scale richness and diversity, in combination with high numbers of undescribed and locally rare taxa (i.e. restricted to one station), infer a degree of isolation and uniqueness in the HIMI benthos. Hence, like Bouvet Island (Gutt *et al.* 2006), 'restricted isolation' may be most appropriate to describe the biogeography of benthic communities at HIMI.

1.5.2 Environmental factors influencing sub-Antarctic benthic invertebrate assemblages

Analysis of these areas has revealed a range of distinctive assemblages, with a conspicuous zonation between the western banks (ABA, CBA and PBA), the central plateau, including Western Plateau and Gunnari Ridge, the Southern Slope, Shell Bank, and waters deeper than 500 m, namely Northeast Plateau. The deeper assemblages tended to have low numbers of taxa and low biomass relative to those of the shallow western banks; the central plateau region and the Southern Slope were diverse, yet inhabited by different species assemblages, and Shell Bank was diverse yet low in biomass compared to the western banks.

Hydrodynamic factors were fundamental to explaining the observed assemblage zonation across HIMI. Of the variables tested, most important was seafloor current speed, particularly to communities on the western banks and Shell Bank. These areas were characterized by high biomasses of sessile suspension-feeding taxa and fast-flowing currents associated with the ACC (van Wijk *et al.* 2010). Particularly noteworthy was the biomass recorded from PBA in depths <300 m owing to large quantities of porifera, serpulidae and ascidiacea (up to 181.6 $g.m^{-2}$). In contrast, shelf habitats within the Atlantic sector of the Southern Ocean recorded up to 408$g.m^{-2}$ (Lockhart & Jones 2008), whilst no more than 42 $g.m^{-2}$ were recorded from the continental shelf along the Great Australian Bite (Long *et al.* 1995), suggesting intermediate biomasses at HIMI, and oceanographic conditions favourable to the formation and maintenance of cold-water sessile suspension-feeding benthos.

A substantial portion of the ACC transport passes in an easterly direction across HIMI and through the Fawn Trough south of Heard Island (Park *et al.* 1991, Park & Gambe´roni 1997, Roquet *et al.* 2009, Park *et al.* 2014) (Fig. 6b). East of GRI, a portion of the Fawn Trough current also diverges from the main flow and moves towards the north-east across SBA (Park *et al.* 2008b). Enhanced species diversity and biomass is commonly associated with seafloor topographies that facilitate locally productive waters by creating barriers to major currents and localised upwellings, such as seamounts and the upstream sides of banks and plateaus (Koslow & Gowlett-Holmes, 1998). In such environments, sessile suspension-feeders often thrive as they depend on the availability of food

suspended in the water column and on the currents for its renewal (Gutt & Starmans 1998, Orejas *et al.* 2000). Hence, the dominance of suspension-feeding communities on HIMI's banks is consistent with patterns documented for banks or seamounts at comparable depths worldwide (e.g. Koslow & Gowlett-Holmes 1998, Stewart *et al.* 2009, Howell 2010).

Fast flowing currents were also common to stations characterized by Assemblage 4 which dominated the south-facing slopes of SSW and had moderate biomasses of serpulids and ascidians. However, it was density of the barnacle *Bathylasma corolliforme* that was most notable; a species common throughout the Southern Ocean (Dayton *et al.* 1982) and particularly prevalent on SSW. In encrusting communities, barnacles such as *B. corolliforme* are among the first colonizers but become replaced by smothering compound and solitary ascidians and encrusting sponges (Chalmer 1982, Harms & Anger 1989). If this pattern of succession is true for HIMI, then SSW may be a recently disturbed community compared to those of the western banks and this could be linked to bottom fishing. For reasons of commercial-in-confidence I cannot present the extent of fishing across HIMI. However certain areas across HIMIs south-facing slopes have been extensively fished, potentially impacting the benthic habitat. Stations characterized by Assemblage 4 had the highest mean values of fishing disturbance (Table 7). Nevertheless, at the scale of HIMI, fishing disturbance was a poor predictor of assemblage distribution. The highest level of disturbance to a station in this study was 2.6 km^2. However, in some areas, the area of seafloor impacted in a single 3 x 3 km cell is > 9 km^2 (i.e. the entire seafloor area within the cell is disturbed by bottom fishing) (Welsford *et al.* 2014b). This highlights the need for further testing of the hypothesis regarding the impact of bottom fishing on sub-Antarctic communities by comparing habitats across a greater range of disturbance.

A high concentration of particulate organic carbon (POC) and low current speeds were common to stations throughout the central plateau. The majority of these stations were characterized by Assemblage 5 which was dominated by echinoderms. Many Antarctic echinoderms, including representatives of the asteroids, ophuroids, echinoids and holothurioiods, are low-energy feeders (i.e. expend very little energy on feeding). Most are opportunistic scavengers (Arnaud 1970, Dearborn 1977, Sloan 1980), and a substantial number exploit detritus or feed on suspended organic material (Dearborn 1977). These feeding strategies make many taxa within the phylum tropically adapted to physically stable, low-energy environment (McClintock 1994), which are common to the Antarctic in depths below 30 m (Dayton 1990, Dayton *et al.* 1994) and supporting their prevalence in Antarctic ecosystems. Their abundance in the central plateau is consistent with the above, being an area of relatively stable oceanographic conditions (Park *et al.* 2008a, Park *et al.* 2008b, van Wijk *et al.* 2010)and high sedimentation (Gutt & Starmans 1998, Gambi & Bussotti 1999). POC is a major food

supply to benthic communities (Vinogradov & Tseitlin 1983) and declines precipitously with depth (Wei *et al.* 2010). Hence, community changes with POC throughout HIMI are likely to be equated to the rate at which the delivery to seafloor declines, and thus the quantity of food available for maintenance of benthic biomass, or specific benthic taxa.

The NEP was characterized by a particularly depauperate, low biomass assemblage which was differentiated by depths >500 m and warmer bottom water temperatures. Changes in species richness and benthic biomass of epifauna with depth are common world-wide (Carney 2005). However, relationships with depth are inevitably complex since depth itself is not a driver. Instead, physical parameters that change with depth, such as seafloor temperature, may influence the suitability of the environment to benthic fauna. As noted above, a portion of the Fawn Trough current moves towards the north-east through the trough between the relatively shallow central plateau and west of Shell Bank (Park *et al.* 2008b). This flow crosses NEP and may explain the warmer bottom water temperatures observed here. However the significance of bottom water temperature on benthic formation in the deep-sea is poorly understood.

Substratum is a dominant factor affecting the distribution and extent of benthic fauna, particularly for sessile taxa that rely on suitable surfaces for settlement (McArthur *et al.* 2009). Insufficient data on the substrate across HIMI meant that it could not be included as a potential environmental variable in this study. However, available sediment data (ODP 1998) and video observations of seafloor (Kilpatrick *et al.* 2011) suggest coarse sediments exist on the tops of the banks and slopes, a unique layer of shellgrit on SBA, and a relatively homogenous substratum of diatomaceous ooze and mud across the central and northeast plateaus which is consistent with the different biological assemblages in each area. High energy areas with strong bottom flows, like the western banks, generally support coarse, poorly sorted sediments, whilst low energy areas, like the central plateau, tend to support sediments with fine grain sizes (Grebmeier *et al.* 1989, Park *et al.* 2008b, van Wijk *et al.* 2010). High biomasses of sessile taxa to the west, and communities of many taxa adapted to low-energy environments with higher sedimentation rates like echinoderms or polychaetes throughout the central plateau, could therefore be linked to differences between the substrates in each area.

1.5.3 Potential ramifications of changing environments

A number of recent studies have demonstrated that the state of the Southern Ocean is changing. Sea surface temperatures near HIMI have risen by at least 0.8 ºC since the 1950s (Ruddell & Allison 1998, Quayle et al. 2002), and in the last 20 years the position of the ACC has shifted polewards by about 60 km altering patterns of flow across the plateau (Sokolov & Rintoul 2009). The

consequences of such changes on HIMI's benthic communities are unknown; although long-term effects are likely given the importance of the ACC to the evolution and maintenance of HIMI's benthic biodiversity. For instance, changing flow patterns may impact recruitment, particularly so for those species without a pelagic larval phase, or survival both in terms of food (e.g. supply of suspended matter) and environment habitability (e.g. availability of hard substrates). If the ACC flow were to completely surpass HIMI, a dramatic change in community structure and function would be likely . However, research now suggests that the topography of the Kerguelen Plateau has such an influence on the ACC that its flow across the plateau will not to shift in the future (Graham *et al.* 2012, Chacko *et al.* 2014). Meaning that environmental conditions and associated biodiversity may remain relative stable into the future; a hypothesis that requires testing to determine its validity and the potential implications on Southern Ocean biodiversity.

1.6 Conclusion

Until now few studies have looked closely at the factors influencing the ecology of deep-sea sub-Antarctic communities, except at the biogeographic level (e.g. Meyer *et al.* 2000, Lockhart & Jones 2008). Importantly, variation in assemblage structure and diversity were observed at the geomorph level (i.e. bank, plateau, slope), with much of this variation explained by just a few key environmental variables. Consequently, management of risks to HIMI needs to be considered at comparable scales to achieve CAR protection of benthic biodiversity. Furthermore, the strong link between the benthic fauna and their environment suggest that long-term changes associated with climate change could have significant effects on patterns of biodiversity throughout the deep sub-Antarctic, substantiating the need to quantify these ecosystems before fast-acting changes confound baseline measurements.

Chapter 2 - A comparison of four models for estimating patterns of vulnerable taxa across the Heard Island and McDonald Islands region

2.1 Abstract

A selection of four models was compared to determine the most appropriate method to model and predict the occurrence probability and biomass of vulnerable taxa across the Heard Island and McDonald Islands (HIMI) region. I contrasted general linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT) and random forests (RF). Models for each method and 10 key vulnerable taxa (i.e. sponges and corals) were constructed using 104 observations and 19 predictor variables. Observations were divided into training and test datasets to facilitate external cross validation. Model performance was then assessed based on two criteria: 1) accuracy of prediction and 2) model calibration and bias. 'Accuracy' meaning the model's ability to discriminate between presence and absence locations and values of biomass for both the training and the independent test data, and 'calibration and bias' meaning how well the frequency of observations in test data agrees with predicted probabilities of occurrence or biomass. According to these indices, RF was the 'best' performing model, resulting in good accuracy, high calibration and low bias. Hence RF was recommended as the preferred model to further explore and predict the distribution and biomass of vulnerable taxa across HIMI.

2.2 Introduction

A vast number of spatial modelling techniques have been applied by ecologist to predict species distributions across aquatic and terrestrial biomes. In general, these models employ correlations between point-data on species occurrence or density (abundance or biomass) and synoptic layers of environmental covariates to predict that species occupancy range and extent at required spatial scales. These models and the estimates they derive have wide management applications in the context of conservation biology, biogeography and climate change studies (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Arau´jo & Rahbek 2006, Meynard & Quinn 2007). However, selecting the most appropriate model to derive robust estimates can be difficult and is often overlooked.

In preparation for modelling vulnerable taxa across the Heard Island and McDonald Islands (HIMI), in this study I trailed a series of commonly applied models to address the following questions:

1) Is there a statistical technique that has a consistently higher predictive ability than others for all kinds of occurrence–environment and biomass-environment relationships? and
2) Is there a statistical technique that is more suited to exploring benthic datasets like HIMI with few observations and frequent non-detections?

Given the large number of modelling strategies available, I restricted the analyses to comparing four commonly used methods (Guisan & Thuiller 2005, Latimer *et al.* 2006, Meynard & Quinn 2007). These included two parametric data models, generalized linear models (GLM, McCullagh & Nelder 1989) and generalized additive models (GAM, Hastie *et al.* 2001), and non-parametric two algorithmic models, boosted regression trees (BRT, Elith *et al.* 2008), and random forests (RF, Breiman 2001a). I used each of these models to evaluate and predict the occurrence probability and biomass of vulnerable taxa, then applied a series of indices to compare and contrast model accuracy. The overall objective was to determine which of these models is ‘best’ to further explore and predict vulnerable marine benthos across marine seascape like HIMI for the purpose of informing management of biodiversity.

2.3 Methods

2.3.1 Sampling

Between April 2003 and May 2008, three shipboard surveys of benthic invertebrate fauna were conducted in the EEZ of HIMI between 49ºS to 57ºS and 67ºE to 80ºE (Fig. 12). A total of 104 samples were collected from nine areas throughout HIMI, selected for the purpose of evaluating regional differences in faunal composition, and to encompass the range of environments and geomorphologies present between 150 and 1000 m depth. They included Aurora Bank (ABA), Coral Bank (CBA), Pike Bank (PBA), Shell Bank (SBA), Northeast Plateau (NEP), Southern Slope West (SSW), Southern Slope East (SSE) and two areas representative of the greater central plateau region, including Western Plateau (WPL) and Gunnari Ridge (GRI). Physical characteristics for each of these areas and the rationale behind their selection are detailed in Chapter 1. Benthic samples were collected using a 2.7 m wide beam trawl fitted with a 1 cm^{-2} net mesh. Thus fauna collected belonged predominantly to the megabenthos, meaning invertebrates usually larger than 1 cm living on or near the sediment surface.

Beam trawl samples were sorted into broad taxonomic groups onboard the vessel and frozen for subsequent analysis. In the laboratory, samples were defrosted and then sieved over a 1 cm mesh prior to sorting and classification. All organisms retained on the sieve were sorted to species, if known, or in most cases operational taxonomic units (OTUs) representative of a species (Blaxter *et al.* 2005). Individuals of all non-colonial taxa were counted individually and then weighed as a group, while colonial taxa were only weighed. Counts and weights were standardised to abundance (number of individuals) and biomass (grams) per square metre of the seafloor ($n.m^{-2}$ and $g.m^{-2}$, respectively) based on the swept area (m^{-2}) of each trawl. Swept area, i.e. the area of seafloor sampled by each trawl, was determined by multiplying trawl distance by the beam trawl width. Trawl distance was calculated as the great circle distance from the start and finish coordinates, which were determined from line tension and vessel position. A systematic description of these samples is presented in Chapter 1.

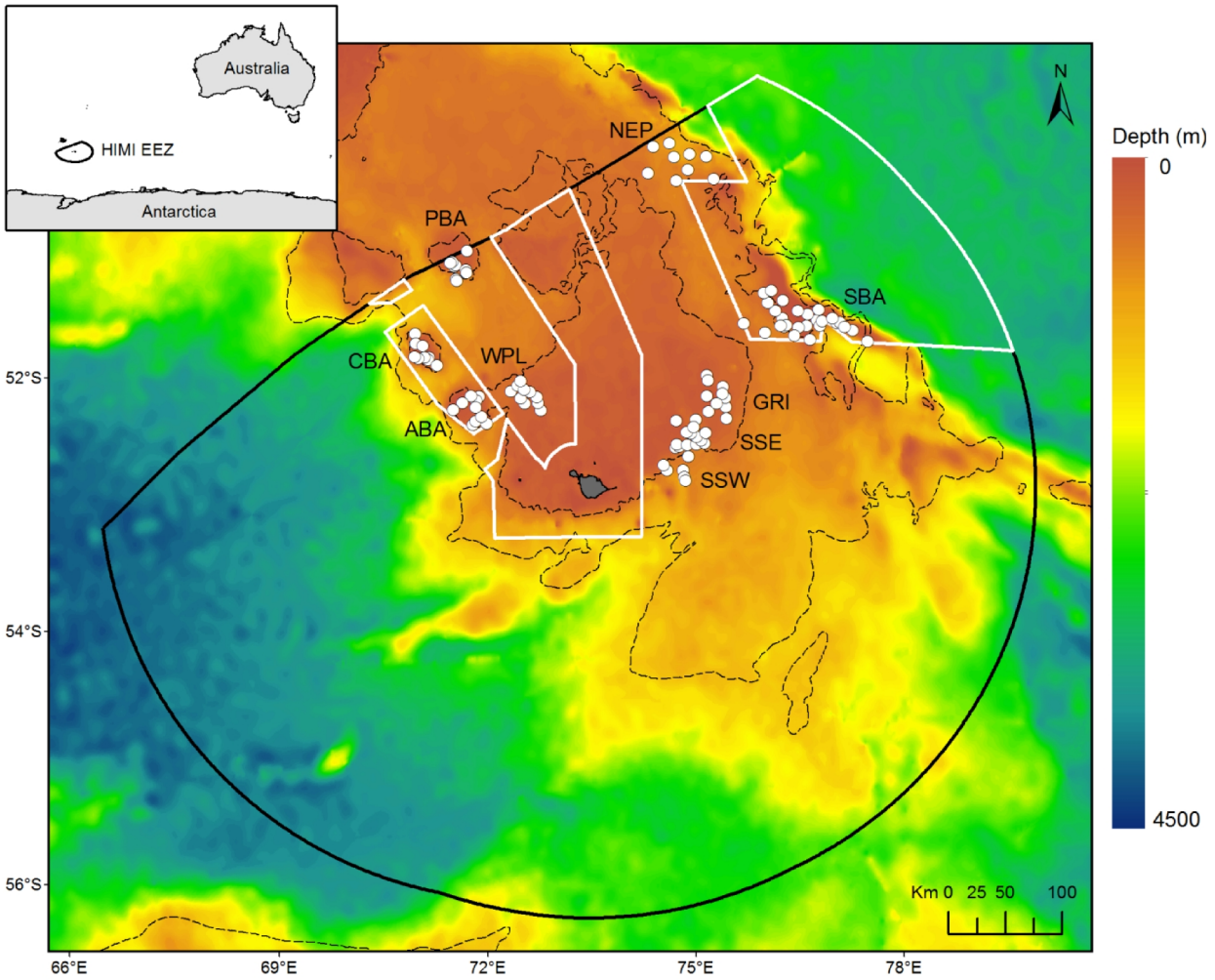

Fig. 12 Location of the Heard Island and McDonald Islands (HIMI) Australian Exclusive Economic Zone (EEZ) and 104 beam trawl sampling stations on the central Kerguelen Plateau. White circles denote individual beam trawls. The white polygons denote the HIMI marine protected area (MPA). The dashed-lines denote the 500 and 1500 m depth contours. Bathymetry from GEBCO One Minute Grid (Last updated in 2008) (GEBCO_08 2008). Areas sampled include Aurora Bank (ABA), Coral Bank (CBA), Pike Bank (PBA), Shell Bank (SBA), Northeast Plateau (NEP), Southern Slope West (SSW), Southern Slope East (SSE), Western Plateau (WPL) and Gunnari Ridge (GRI).

2.3.2 Data on vulnerable taxa and considerations for modelling

Benthic fauna were considered "vulnerable" if their morphological or life-history characteristics meant they were susceptible to damage or mortality upon an interaction with a bottom-fishing gear. For example, deep-sea corals, which are slow-growing, long-lived, tall and brittle, are damaged or destroyed by bottom fishing (Roberts & Hirshfield 2004). A review of the HIMI dataset identified 18 "vulnerable taxa" (Table 10). Sessile, suspension-feeding invertebrates, such as sponges and corals, comprised the majority of vulnerable taxa. Not only are these sessile fauna vulnerable due to their morphology (e.g. emergent and brittle) and low recovery potential (i.e. slow-growing and long-lived), they are also important ecosystem engineers (Hiefetz 2002, Puniwai 2002, Tissot *et al.* 2004a, Auster 2005a), providing relief and living habitat for fish and other invertebrates. These sessile fauna

are also those specifically mentioned by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) as indicators of vulnerable marine ecosystems (VME) in the Southern Ocean (CCAMLR 2009b). Understanding the distribution of these vulnerable taxa with respect to the distribution of fishing activity is therefore important to the management and conservation of HIMI's marine biodiversity.

Prior to modelling, data on vulnerable taxa was scrutinised to determine its applicability for assessment and prediction. Firstly, most vulnerable taxa were colonial therefore density estimates will focus on biomass ($g.m^{-2}$). Secondly, several taxa were restricted to only a few samples and hence, to allow adequate data for model training, only taxa present at >50% of the stations were assessed (see Table 10). In addition, the clumped distribution of samples means that spatial autocorrelation may be encountered, and if not properly addressed, may influence the statistical inference of the models (Lichstein *et al.* 2002, Dormann 2007, Dormann *et al.* 2007). I explored whether there was spatial autocorrelation in the data for each vulnerable taxa assessed by calculating Moran's *I* (Moran 1950) and Geary's *C* (Geary 1954) for the 50 nearest neighboring samples using the functions *moran.test* and *geary.test*, respectively, in the R package *spdep* (Bivand et al. 2013a, Bivand & Piras 2015).

Table 10 List of vulnerable taxa assessed in the HIMI region. Taxa used in further analysis and prediction are shaded grey. 'Presence' is the number of beam trawl events out of 104 conducted across the HIMI region in which they were captured.

Phylum	Taxon	Common name	Presence
Porifera	Demospongiae	bath or siliceous sponges	91
	Hexactinellida	glass sponges	33
Cnidaria	Actinaria	anemones	71
	Alcyonacea	soft corals or alcyonarians	69
	Gorgonacea	horny corals or gorgonians	64
	Hydrozoa	hydroids or sea ferns	87
	Scleractinia	hard corals	42
	Pennatulacea	sea pens	2
	Zoantharia	zoanthids	9
	Hydrocorallia	hydrocorals	16
Annelida	Serpulidae	serpulid tube worms	69
Bryozoa	Bryozoa	lace coral	72
Brachiopoda	Brachiopoda	lamp shells	51
Arthropoda	Cirripedia	stalked barnacles	58
Echinodermata	*Ctenocidaris nutrix*	pencil urchin (echinoidea)	63
	Euryalida	snake or basket stars	43
Hemichordata	Pterobranchia	pterobranchs	35
Chordata	Ascidiacea	sea squirts	84

2.3.3 Environmental data and fishing effort

Nineteen predictor variables with coverage across HIMI that are either known or suspected to be correlated with the distribution of benthic fauna were considered in this model-evaluation (Table 11). Values for each parameter were extracted at the midpoint (latitude/longitude) of each beam trawl track using the software package ESRI ArcGIS v10.1.Prior to modelling, these variables were subjected to a selection process to eliminate highly correlated variables, since regression-based models are sensitive to correlations between variables. First, all variables were normalized to a common scale after log transformation of skewed variables. Pairwise linear regressions were then calculated between all normalized variables to identify (if any) highly correlated variables. High correlations (i.e. correlation values $|r| > 0.85$) were found between (a) *poc* and *chl*, and (b) *dist.isl*, *dist.can* and *mld* (abbreviations as per Table 11); only one of each group was included in the analysis. Variables retained were *poc* and *dist.isl*; *poc* for its relevance to benthic productivity at the seafloor and *dist.isl* as a proxy for distance to islands. Thus, the final models included 16 predictor variables.

Table 11 Datasets of predictor variables across HIMI including environmental parameters and fishing effort.

Variable	Short	Unit	Variable layer description	Reference
Surface water				
Chlorophyll *a*	chl	mg m^{-3}	Average of annual values from the MODIS (Moderate Resolution Imaging Spectroradiometer) aqua mission data from July 2009 to December 2008.	Feldman and McClain (2010)
Sea surface temperature	sst	°C		
Mixed layer depth	mld	m	Annual mean concentration derived from the CSIRO Atlas of Regional Seas (CARS 2009).	Condie and Dunn (2006)
Bottom water				
Particulate organic carbon	poc	mg m^{-3}	Average of annual values from the MODIS aqua mission data from July 2009 to December 2008. Values at the seafloor were approximated on the basis MODIS particulate organic carbon data and variations in water depth.	Stramski *et al.* (2008)
Temperature	btm.tmp	°C	Annual mean concentration derived from CARS 2009.	Ridgway *et al.* (2002)
Dissolved oxygen	btm.oxy	ml l^{-1}		
Nitrate	btm.nit	µmol l^{-1}		
Phosphate	btm.pho	µmol l^{-2}		
Silicate	btm.sil	µmol l^{-1}		
Salinity	btm.sal	PPS		
Physical				
Seafloor current speed	btm.spd	m s^{-1}	Current speed near the seafloor averaged over 12 snapshots from the CAISOM ocean model.	Galton-Fenzi *et al.* (2012)
Seafloor vertical velocity	btm.vvl	m s^{-1}	Vertical velocity at the seafloor averaged over 12 snapshots from the CAISOM ocean model.	
Seafloor slope	slope	m	Slope values calculated from the Kerguelen Digital Elevation Model (KDEM).	Beaman and O'Brien (2011)
Seafloor aspect	aspect	m	Aspect values calculated from the KDEM.	
Distance				
Distance to sub-Antarctic island	dist.isl	km	Distance to nearest land mass north of 65°S calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km.	Australian Antarctic Data Centre (AADC)
Distance to canyon axe	dist.can	km	Distances to nearest canyon axis calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from O'Brien and Post's (2009) seafloor geomorphology data.	AADC, O'Brien *et al.* (2009)
Distance to shelf break	dist.shf	km	Distance to nearest area of sea floor of depth 500 m or less. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from ETOPO1 bathymetry data.	AADC, Smith and Sandwell (1997)
Water depth				
Depth	depth	m	Depth estimated from the KDEM.	Beaman and O'Brien (2011)
Fishing effort				
Fishing effort	effort	km^2	Total fishing effort per cell expressed as the sum of area impacted by one fishing event, two fishing events to *n* fishing events. Only fishing events that occurred prior to benthic sample collections were considered. See Chapter 1 for further detail on the calculation of effort for each beam trawl track.	Welsford *et al.* (2014b)

2.3.4 Model construction

I constructed two sequential models; one to predict the occurrence probability of each vulnerable taxa (termed 'occurrence model'), and one to predict the biomass of that vulnerable taxa given their presence in an area (termed 'biomass model'). Models of benthic fauna across marine seascapes are often restricted to estimates of presence only. But in the development of MPAs, identification criteria depend not only on the presence of biota, but also on their density in an area (biomass or abundance), since density will influence ecosystem structure and function, potential as a food or habitat resource, and vulnerability to anthropogenic activities. Hence, useful models must predict both occurrence and density, represented as biomass in this study. Also by fitting these models in an hierarchical fashion, skewed distributions with frequent non-detections (zeros), which are common in ecological data, were also accounted for (Potts & Elith 2006, Wenger & Freeman 2008, Millar 2009). All models were constructed in R 3.2.0 with the packages *mgcv* (Wood 2000), *gbm* (Ridgeway 2015), *randomForest* (Liaw & Wiener 2002) and *dismo* (Hijmans *et al.* 2011).

For the occurrence models, I used the Bernoulli distribution for BRT and the binomial distribution for the parametric models GLM and GAM. For the biomass models, I used the same modelling techniques as for occurrence, except I used the quasi-Poisson distribution for the parametric models since the response variable is not strictly a count. Hence, the quasi-Poisson error distribution was considered a reasonable approach given that standard errors of parameters accounted for the estimated dispersion parameter which could be greater than or less than 1. The estimated dispersion parameter was obtained as the residual deviance divided by its degrees of freedom.

Models for each method (GLM, GAM, BRT and RF) and both the occurrence and biomass modelling frameworks included all 104 observations and 19 predictor variables. Swept area (log m^{-2}) was also included as an offset in the model to account for sampling intensity.

2.3.5 Model evaluation and calibration

The beam trawl data was divided into training and test data by randomly setting aside approximately 25% of the survey data (26 beam trawl samples) for external cross validation. This division provided adequate occurrence and biomass data for all taxa to allow model testing, although the robustness of these investigations was limited by the relative small sample size of 104.

Model performance was assessed based on two criteria: 1) accuracy of prediction and 2) model calibration and bias. 'Accuracy' meaning the model's ability to discriminate between presence and absence locations and values of biomass for both the training and the independent test data, and

'calibration and bias' meaning how well the frequency of observations in test data agrees with predicted probabilities of occurrence or biomass.

For the occurrence models, accuracy was reported as the area under the receiver-operating characteristic curve (AUC). AUC ranges from 0 to 1, with values >0.9 indicating excellent accuracy, values between 0.7–0.9 considered as useful, and below 0.6 indicating a performance no better than random. AUC values were calculated using the package *PresenceAbsence* (Freeman & Moisen 2008) in R 3.2.0. To test calibration and bias, I used a linear regression of the relative frequency of observed presences over ten bins of predicted probabilities of presence implemented in a binned calibration plot using the *plots.R* (Phillips & Elith 2010) function in R. The slope and the intercept of this regression indicate the calibration and the bias of the model, respectively (Phillips and Elith, 2010). In addition, I calculated the point-biserial correlation between predicted and observed values, which is sensitive to both discrimination and calibration. For biomass models, I used the Pearson correlation coefficient and the slope and intercept of a major axis regression of observed over predicted values to evaluate the bias and consistency of model predictions (Potts & Elith 2006, Pineiro *et al.* 2008). Accuracy is reported as the percent variance explained (R^2), with higher values of R^2 indicating better model performance. Results of these model comparisons are presented as the mean across all 10 vulnerable taxa.

2.4 Results and Discussion

2.4.1 Spatial autocorrelation

For the HIMI dataset there was little evidence for spatial autocorrelation in either the occurrence (Moran's I = 0.018 ± 0.017 standard deviation, SD; Geary's C = 0.98 ± 0.03 SD) or the biomass (Moran's I = 0.021 ± 0.017 SD; Geary's C = 1.02 ± 0.11 SD) of vulnerable taxa (Table 12). Hence, I did not specifically incorporate measures to account for spatial autocorrelation in the model, but note that methods to incorporate spatial autocorrelation have recently become available (Hothorn *et al.* 2011).

Table 12 Spatial autocorrelation in data for the (1) occurrence and (2) biomass of each vulnerable taxa assessed using Moran's *I* and Geary's *C*. Moran's *I* ranges from -1 (perfect dispersion) to +1 (perfect correlation), with values around zero indicative of a random spatial pattern. Geary's C ranges from 0 to 2, with values around 1 indicative of a random spatial pattern.

	Moran *I*		**Geary's *C***	
Taxa	*Occurrence*	*Biomass*	*Occurrence*	*Biomass*
Demospongiae	0.0071	0.0486	0.9513	0.0018
Gorgonacea	0.0031	0.0364	0.9826	0.0021
Alcyonacea	-0.0167	-0.003	0.9953	0.0021
Hydrozoa	0.0015	-0.0136	0.9747	0.0039
Actinaria	0.0266	-0.0205	0.9574	0.0007
Serpulidae	-0.0217	0.0059	0.9999	0.0048
Bryozoa	-0.0247	0.0122	0.9983	0.0017
Cirripedia	-0.0185	-0.0013	1.0052	0.0041
C. nutrix	-0.0007	0.0186	0.9913	0.0033
Ascidiacea	0.0586	0.0455	0.9283	0.0028

2.4.2 Performance of the occurrence and biomass models

All four models had reasonable ability to discriminate between areas where vulnerable taxa were present and absent (all AUC > 0.75, Fig. 13). For the training data used to construct the models, RF and BRT provided the best discrimination between presence and absence locations (highest AUC and correlation). RF was the best-correlated model, and BRT was the best-calibrated. GLMs and GAMs performed well, but were less accurate, and more weakly calibrated, than RF and BRT.

By contrast, prediction accuracy for the independent test data was very similar among the four modelling techniques (i.e. similar average AUC and correlation values). BRT was the best calibrated model but had the highest biomass. Calibration and bias was similar among RF, GLM and GAM.

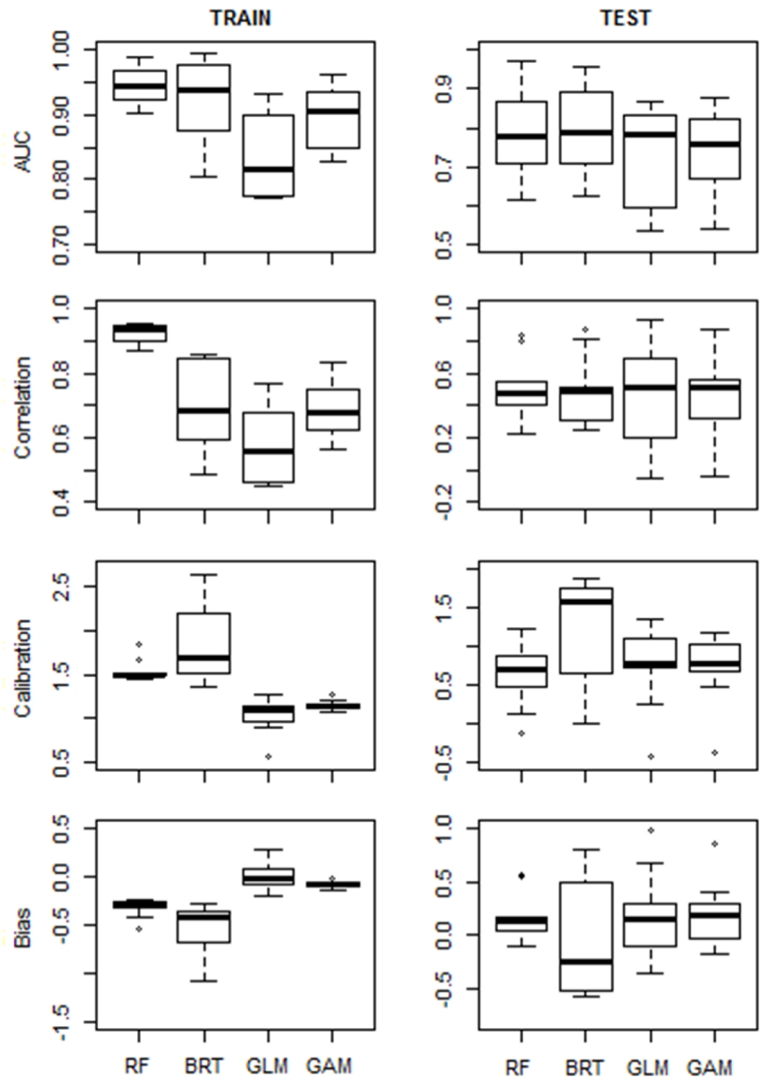

Fig. 13 Plot of model statistics for occurrence models for training and independent test data. Models were computed for each vulnerable taxa using Random Forests (RF), Boosted Regression Trees (BRT), Generalised Linear Models (GLM) and Generalised Additive Model (GAM). Statistics include area under the receiver-operating characteristic curve (AUC), point-biserial correlation between observed and predicted values (COR), model calibration and bias. Box plots indicate median (central line), 25% and 75% percentiles (lower and upper line of the box), 10% and 90% percentiles (lower and upper limit of the vertical bar), and single values outside the 10% and 90% limits (circles). BRT test calibration and bias value for Hydrozoa was removed due to being a major outlier.

As with the occurrence models, performance of biomass models was very different between training and independent test data (Fig. 14). For the training data, RF and GAM explained the most amount of variation in vulnerable taxa biomass, and showed the highest correlation between observed and predicted values, followed closely by GLMs. BRT was again the best calibrated model, but suffered from relatively large bias.

For the test data, the parametric models (GLM and GAM) and RF were the best performing models according to mean R^2 and correlation values, whilst BRTs continued to suffer from high bias. However, performance was highly variable among taxa, with R^2 values ranging between 0.2 and 0.9. The reliability of these models' estimates was therefore highly taxa-dependent.

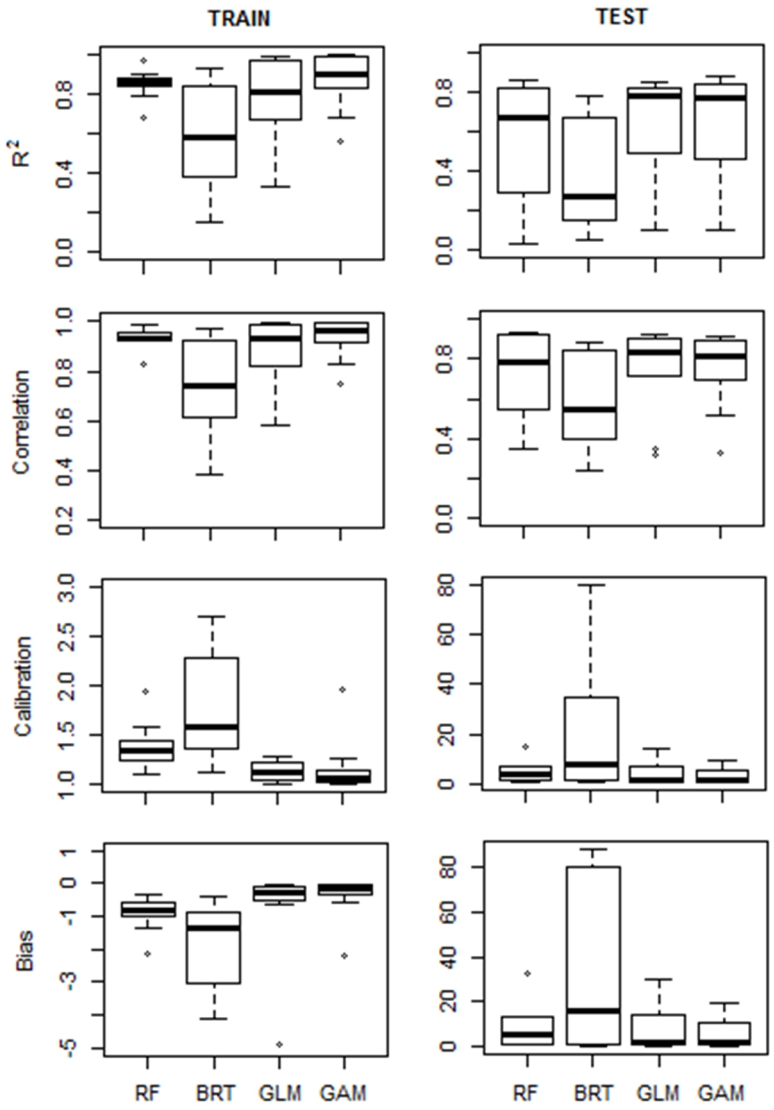

Fig. 14 Plot of model statistics for biomass models for training and independent test data. Models were computed for each vulnerable taxa using Random Forests (RF), Boosted Regression Trees (BRT), Generalised Linear Models (GLM) and Generalised Additive Model (GAM). Statistics include Pearson's correlation between observed and predicted values (COR), percent variance explained (R^2), model calibration and bias. Box plots indicate median (central line), 25% and 75% percentiles (lower and upper line of the box), 10% and 90% percentiles (lower and upper limit of the vertical bar), and single values outside the 10% and 90% limits (circles). BRT test calibration and bias values for Hydrozoa, Cirripedia and Bryozoa were removed due to being major outliers.

2.4.3 Final model selection

According to the indices and data used, RF and BRT would be the preferred choice for estimating occurrence probability, whilst RF, GLM and GAM were best suited to the biomass data. In this evaluation, biomass model predictions are reliant on the predictive ability of the occurrence model of the same technique (i.e. biomass was the product of predicted probability of occurrence and predicted biomass). For this reason, RF is recommended as the preferred model to further explore and predict the distribution and biomass of vulnerable taxa throughout HIMI. In addition, unlike parametric models, RF does not require formal selection of predictors, does not assume any data distribution, is robust to outlier and unbalanced data, and cross-validation with external data is not necessary due to internal bootstrapping (Breiman 2001a). As such, non-parametric models like RF are now considered a better choice than traditional statistical methods (Cutler & Stevens 2006). In

instances like HIMI with few observations, and where the relationships between benthic invertebrate distributions and their environments are complex, and in many cases still poorly understood, RF may be a better choice to model and predict the spatial distribution of benthic biodiversity.

Chapter 3 - Improving protection of benthic biodiversity in the deep Southern Ocean using predictions of occurrence and biomass

3.1 Abstract

Knowledge about the spatial distribution of benthic habitats is important for marine conservation planning, particularly where areas of resource exploitation may overlap with areas of high conservation value, as in the case with bottom fishing in the Southern Ocean. In high latitude, deep-sea regions such as the Southern Ocean, data on the benthos covers only a subset of the areas targeted by fisheries making informed management decisions challenging. In such situations, the spatial distribution of biota is frequently inferred from predictive statistical models to assist with planning and management. Here I employed the machine-learning algorithm, Random Forests, to model and predict the probability of occurrence and biomass of 'vulnerable taxa' across the Heard Island and McDonald Islands (HIMI) region. Bottom fishing has occurred at HIMI since 1997, with potential impacts mitigated through a substantiative marine protected area (MPA) and yet the representativeness of the MPA for high conservation value benthic assemblages remains largely unknown. Models were constructed for 10 vulnerable taxa with predictions then analysed using the algorithm *Zonation* to identify priority areas for conversation. Data on benthic biodiversity, distribution and biomass that were used to construct the model came from 104 beam trawl samples and 19 environmental predictor variables. Model predictions were highly variable across the HIMI seascape, although most vulnerable taxa occurred more frequently, and at higher biomasses, in shallower depths (<400 m), and on complex seascapes (e.g. banks/seamounts or craggy slopes). A high occurrence probability did not always coincide with a high biomass, highlighting the importance of considering estimates of both occurrence and biomass in marine conservation planning. Areas of high conservation priority for vulnerable taxa were well represented in the HIMI MPA, although some areas outside the MPA may warrant further investigation. This study presents a comprehensive approach to modelling for the purposes of identifying high conservation value assemblages in areas where bottom fisheries occur, and which should be readily transferable to other areas.

3.2 Introduction

Fisheries deploying bottom-contacting gears have the potential to cause significant adverse impacts to benthic marine habitats. Destruction of benthic habitat structure (Koslow *et al.* 2001), local extinction of species (Hiddink *et al.* 2006) and even wholesale shifts in the functioning of entire ecosystems (Kaiser *et al.* 2000, Jennings *et al.* 2001) are among a range of impacts directly linked to bottom fishing. Reducing impacts to benthic habitats and other marine biodiversity may be achieved by the designation and enforcement of marine protected areas (MPAs).

Identifying candidate areas that are suitable for protection of benthic habitats requires a thorough understanding of the spatial distribution of benthic biodiversity. Many of Earth's near shore, shallow-water habitats are well described due to their accessibility, ease of study and proximity to anthropogenic threats. In contrast, benthic habitats in high latitude, deep-sea regions, such as the Southern Ocean, are poorly described despite established bottom fisheries (Constable & Holt 2007, Bensch *et al.* 2009). A description of these habitats is important to assist with managing biodiversity in deep-sea regions, particularly where use of bottom-contacting gears may overlap areas with high conservation value.

Studies to determine the spatial distribution of benthic biodiversity in deep-sea regions are complicated by high costs and difficulties associated with working in these remote and often extreme environments. Because of this, surveys are usually limited to restricted areas of interest and small sample sizes which tend to fall short of the spatial distribution of fisheries targeting these habitats. An alternative approach to deriving the distribution of benthic biodiversity across large spatial scales is to base species or habitat predictions on the relationship between organisms and their environment using statistical modelling techniques (Meynard & Quinn 2007, McArthur *et al.* 2010). The study of benthic habitats and their distributions has often focused on the association between biodiversity and components of the physical habitat (Hixon *et al.* 1991b, Stein 1992, Yoklavich *et al.* 2000, Nasby-Lucas *et al.* 2002, Auster 2005a, Grant *et al.* 2006). However, only recently, with the increasing availability of large-scale remote sensing data which can provide environmental predictor variables, have scientists been able to better characterise these relationships to create robust predictive models of benthic faunal diversity, biomass or abundance as a function of environmental gradients (Brodeur 2001, Ysebaert & Herman 2002, Thrush *et al.* 2003, Guisan & Thuiller 2005, Elith *et al.* 2006, Oppel & Huettmann 2007).

Traditionally, most species or habitat predictions have been based on statistical data models such as generalized linear models (GLM). More recently, however, the use of algorithmic models has been advocated for ecological studies (Cutler *et al.* 2007, Hochachka *et al.* 2007, Elith *et al.* 2008).

Algorithmic models derived from machine learning theory have been shown to be superior to conventional data models in modelling the distribution of terrestrial animals (Elith *et al.* 2006, Prasad *et al.* 2006), but their use in marine ecosystems has been limited so far (Denisenko *et al.* 2003, Leathwick *et al.* 2006). The key difference between data models like GLMs and algorithmic models is that algorithmic models do not require the relationship between dependent variables such as the occurrence or biomass of benthic invertebrates and explanatory variables like depth to be specified, but rather start virtually uninformed and use an algorithm to learn these relationships. Algorithmic models can thus elucidate extremely complex and unanticipated relationships in a dataset that might otherwise be missed where variables and relationships are specified through human selection (Breiman 2001b). As the relationships between benthic invertebrate distributions and their environments are complex, and in many cases still poorly understood, algorithmic models may be the better choice to model and predict the spatial distribution of benthic invertebrates across large spatial scales in marine ecosystems (Wei *et al.* 2010).

In this study I use a Random Forests algorithm (Breiman 2001a) to model and predict the spatial distribution of benthic fauna across the Heard Island and McDonalds Islands (HIMI). Since April 1997 an Australian bottom fishery targeting Patagonian toothfish (*Dissostichus eleginoides*) in deep waters (> 500 m) has been in operation in the HIMI region with consequent impacts to the benthic habitat. Early development of a substantial MPA in 2002 within the HIMI Exclusive Economic Zone (EEZ) was an integral part of the recognition and mitigation for benthic impacts in the HIMI fishery. Chapter 1 has identified a diverse and complex array of benthic habitats with a range of slow-growing and potentially vulnerable taxa. However, an analysis of the spatial distribution of biodiversity in areas where fishing occurs, but samples have not been collected, is required to determine whether the MPA is meeting CAR (comprehensive, adequate and representative) principles for benthic biodiversity at HIMI.

3.3 Methods

3.3.1 Data on vulnerable benthic invertebrate taxa

Biomass data ($g.m^{-2}$) for 104 beam trawl samples were used to parameterise models of benthic fauna throughout the HIMI region (Fig. 15). These 104 samples were collected between April 2003 and May 2008 from a range of environments and geomorphologies present between 150 and 1000 m depth across HIMI. Areas sampled included Aurora Bank (ABA), Coral Bank (CBA), Pike Bank (PBA), Shell Bank (SBA), Northeast Plateau (NEP), Southern Slope West (SSW), Southern Slope East (SSE) and two areas representative of the greater central plateau region, including Western Plateau (WPL) and Gunnari Ridge (GRI) (Fig. 15). Physical characteristics for each of these areas and the rationale behind their selection are detailed in Chapter 1, which also provides a systematic description of the processing and faunal composition of each of the 104 samples. Benthic samples were collected using a 2.7 m wide beam trawl fitted with a 1 cm^{-2} net mesh. Thus fauna collected belonged predominantly to the megabenthos, meaning invertebrates usually larger than 1 cm living on or near the sediment surface.

Estimates will focus on those megabenthos considered most vulnerable to damage or mortality upon an interaction with a bottom-fishing gear. A review of the HIMI dataset in Chapter 2 identified 18 'vulnerable taxa' although only 10 will be used for modelling and prediction due to insufficient observations of the remaining taxa (i.e. <50 observations) (Table 13). Sessile, suspension-feeding invertebrates, such as sponges and corals, comprised the majority of vulnerable taxa. Not only are these sessile fauna vulnerable due to their morphology (e.g. attached, emergent and brittle) and low recovery potential (i.e. slow-growing and long-lived), they are also important ecosystem engineers (Hiefetz 2002, Puniwai 2002, Tissot *et al.* 2004a, Auster 2005a), providing relief and living habitat for fish and other invertebrates. For example, deep-sea corals, which are brittle, slow-growing, long-lived and provided the basic habitat structure for many benthic invertebrate fauna and fishes, are damaged or destroyed by bottom fishing (Roberts & Hirshfield 2004). These sessile fauna are also those benthic fauna specifically mentioned by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) as indicators of vulnerable marine ecosystems (VME) in the Southern Ocean (CCAMLR 2009b). Understanding the distribution of these vulnerable taxa with respect to the distribution of fishing activity is therefore important to the management and conservation of HIMIs marine biodiversity.

Also on CCAMLRs list of VME indicator fauna is the echinoid taxon *Ctenocidaris nutrix*. *C. nutrix* is from the subclass Cidaroidea (Cidaroids) which includes a large number of species whose

multidimensional array of spines provide suitable microhabitats for a wide diversity of sessile macro-organisms (sponges, bryozoans, molluscs, hydrozoans and similar "fouling" or encrusting organisms) (Heterier *et al.* 2008, Linse *et al.* 2008, Hardy *et al.* 2010). Because of this, cidaroids are often considered 'key' contributors to local benthic diversity; the contribution exceeding their own richness and abundance values (Saucède *et al.* 2014b). Cidaroids are they slow-moving and fragile, meaning that they unable to evade bottom-fishing gears which may damage or dislodge their spines upon impact. Thus, both in structure and function (i.e. as ecosystem engineers), cidaroids like *C. nutrix* are vulnerable to impacts from bottom-fishing gears and hence form an important part of this study.

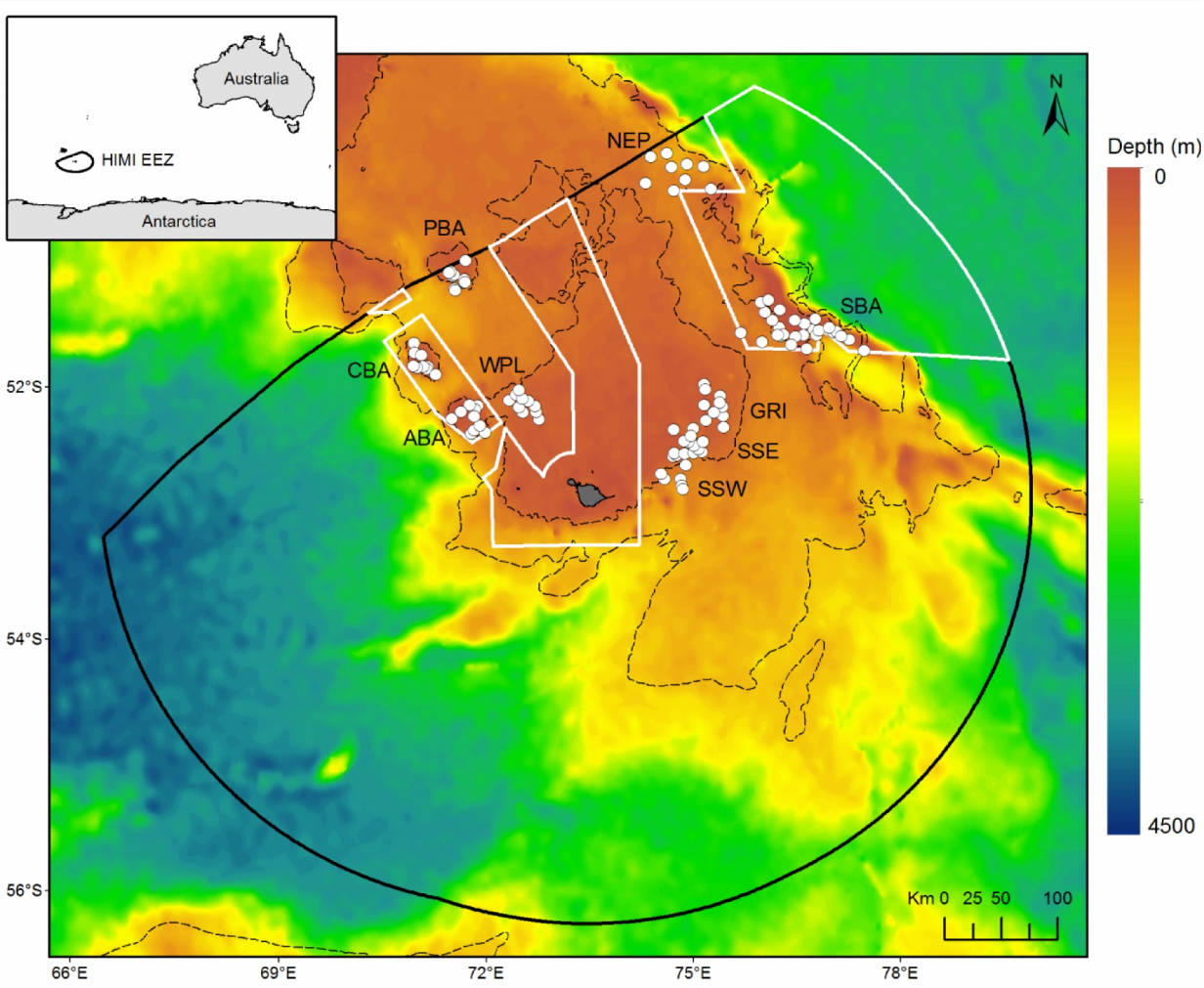

Fig. 15 Location of the Heard Island and McDonald Islands (HIMI) Australian Exclusive Economic Zone (EEZ) and 104 beam trawl sampling stations on the central Kerguelen Plateau. White circles denote individual beam trawls. The white polygons denote the HIMI marine protected area (MPA). The dashed-lines denote the 500 and 1500 m depth contours. Bathymetry from GEBCO One Minute Grid (Last updated in 2008) (GEBCO_08 2008). Areas sampled include Aurora Bank (ABA), Coral Bank (CBA), Pike Bank (PBA), Shell Bank (SBA), Northeast Plateau (NEP), Southern Slope West (SSW), Southern Slope East (SSE), Western Plateau (WPL) and Gunnari Ridge (GRI).

Table 13 List of vulnerable taxa assessed in the HIMI region. All taxa are sessile suspension-feeders other than *Ctenocidaris nutrix* which is listed by CCAMLR as an indicator taxa for VMEs (CCAMLR 2009b). 'Presence' is the number of beam trawl events out of 104 conducted across the HIMI region in which they were captured.

Phylum	Taxon	Common name	Presence
Porifera	Demospongiae	bath or siliceous sponges	91
Cnidaria	Actinaria	anemones	71
	Alcyonacea	soft corals or alcyonarians	69
	Gorgonacea	horny corals or gorgonians	64
	Hydrozoa	hydroids or sea ferns	87
Annelida	Serpulidae	serpulid tube worms	69
Bryozoa	Bryozoa	lace coral	72
Arthropoda	Cirripedia	stalked barnacles	58
Echinodermata	*Ctenocidaris nutrix*	pencil urchin	63
Chordata	Ascidiacea	sea squirts	84

3.3.2 Predictor variables including environmental parameters and fishing effort

The models used 19 predictor variables with coverage across HIMI that are either known, or suspected to be correlated with the spatial distribution and density of benthic fauna to model the distribution of vulnerable taxa. These 19 variables were utilized to categorize six predictor categories (Table 14). Categories included:

1) Sea surface properties relating to phytoplankton productivity, including estimates of particulate organic carbon, the major food supply to benthic communities (Vinogradov & Tseitlin 1983);
2) Bottom water properties characterising seafloor habitats;
3) Physical properties relating to seabed structure and relief;
4) Distance as a proxy to point source influences (i.e. canyons);
5) Water depth; and
6) Fishing effort as a proxy for disturbance to the seafloor habitats.

All layers were compiled in the software package ESRI ArcGIS v10.1 where they were reclassified to a consistent 9 km^2 grid using bilinear interpolation for analysis and prediction. The mean tow length of beam trawls was 1.55 km, with a maximum length of 2.9 km. Consequently, the grid cell size chosen to standardise the values of environmental variables was 3 × 3 km or 9 km^2. Values for each parameter were extracted from the 9 km^2 grid cell containing the midpoint (latitude/longitude) of each beam trawl track.

Table 14 Datasets of environmental predictor variables across HIMI.

Variable	Short	Unit	Variable layer description	Reference
Surface water				
Chlorophyll *a*	chl.a	mg m^{-3}	Average of annual values from the MODIS (Moderate Resolution Imaging Spectroradiometer) aqua mission data from July 2009 to December 2008.	Feldman and McClain (2010)
Sea surface temperature	sst	°C		
Mixed layer depth	mld	m	Annual mean concentration derived from the CSIRO Atlas of Regional Seas (CARS 2009).	Condie and Dunn (2006)
Bottom water				
Particulate organic carbon	poc	mg m^{-3}	Average of annual values from the MODIS aqua mission data from July 2009 to December 2008. Values at the seafloor were approximated on the basis MODIS particulate organic carbon data and variations in water depth.	Stramski *et al.* (2008)
Temperature	btm.tmp	°C	Annual mean concentration derived from CARS 2009.	Ridgway *et al.* (2002)
Dissolved oxygen	btm.oxy	ml l^{-1}		
Nitrate	btm.nit	µmol l^{-1}		
Phosphate	btm.pho	µmol l^{-2}		
Silicate	btm.sil	µmol l^{-1}		
Salinity	btm.sal	PPS		
Physical				
Seafloor current speed	btm.spd	m s^{-1}	Current speed near the seafloor averaged over 12 snapshots from the CAISOM ocean model.	Galton-Fenzi *et al.* (2012)
Seafloor vertical velocity	btm.vvl	m s^{-1}	Vertical velocity at the seafloor averaged over 12 snapshots from the CAISOM ocean model.	
Seafloor slope	slope	m	Slope values calculated from the Kerguelen Digital Elevation Model (KDEM).	Beaman and O'Brien (2011)
Seafloor aspect	aspect	m	Aspect values calculated from the KDEM.	
Distance				
Distance to sub-Antarctic island	dist.isl	km	Distance to nearest land mass north of 65°S calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km.	Australian Antarctic Data Centre (AADC)
Distance to canyon axe	dist.can	km	Distances to nearest canyon axis calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from O'Brien and Post's (2009) seafloor geomorphology data.	AADC, O'Brien *et al.* (2009)
Distance to shelf break	dist.shf	km	Distance to nearest area of sea floor of depth 500 m or less. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from ETOPO1 bathymetry data.	AADC, Smith and Sandwell (1997)
Water depth				
Depth	depth	m	Depth estimated from the KDEM.	Beaman and O'Brien (2011)
Fishing effort				
Fishing effort	effort	km^2	Total fishing effort per cell expressed as the sum of area impacted by one fishing event, two fishing events to *n* fishing events. Only fishing events that occurred prior to benthic sample collections were considered. See Chapter 1 for further detail on the calculation of effort for each beam trawl track.	Welsford *et al.* (2014b)

3.3.3 Model construction, evaluation and prediction

Prior to modelling, consideration was given to the type and distribution of the HIMI data, including potential issues of spatial autocorrelation, and the performance of four alternative methods for predicting vulnerable taxa; generalized linear models (GLM, McCullagh & Nelder 1989), generalized additive models (GAM, Hastie *et al.* 2001), Boosted Regression Trees (BRT, Elith *et al.* 2008) and Random Forests (RF, Breiman 2001a). In summary, I found little evidence for spatial autocorrelation in data, and the ensuing comparison of models identified RF as the preferred model to further explore and predict vulnerable taxa throughout HIMI (Chapter 2).

RF is an algorithmic model which uses machine learning to build an ensemble of decision trees to arrive at correlations between predictor and response variables. Each tree is grown from a bootstrap sample of the response variable and each node is guided by a predictor value to maximize differences in offspring branches and predictive accuracy (Breiman 2001a). The fit of the tree is examined using the data not in the bootstrap selection (termed 'out-of-bag' data, OOB) and hence cross-validation with external data is not necessary. At the same time, RF does not assume any data distribution, does not require formal selection of predictors and is robust to outlier and unbalanced data. As such, RF is considered a better choice than traditional statistical methods (Cutler & Stevens 2006) and is now used widely for data mining, particularly in the fields of bioinformatics (Cutler & Stevens 2006), speech recognition (Xu 2004), and drug design and development (Svetnik *et al.* 2003). Recently RF has gained popularity in terrestrial ecology (Prasad *et al.* 2006, Cutler *et al.* 2007, De'ath 2007) however, only a handful of studies have applied RF in marine ecosystems (Oppel & Huettmann 2010, Wei *et al.* 2010).

The framework trialled in this study consisted of two sequential RF models, one to predict the occurrence probability of each vulnerable taxa (termed 'occurrence model'), and one to predict the biomass of that vulnerable taxa given their presence in an area (termed 'biomass model'). Models of benthic fauna across marine seascapes are often restricted to estimates of presence only. But in the development of MPAs, identification criteria depend not only on the presence of biota, but also on their density in an area (e.g. biomass), since density will influence ecosystem structure and function, potential as a food or habitat resource, and vulnerability to anthropogenic activities. Hence, useful models must predict both occurrence and density. Also, by fitting these models in an hierarchical fashion, skewed distributions with frequent non-detections (zeros), which are common in ecological data, were also accounted for (Potts & Elith 2006, Wenger & Freeman 2008, Millar 2009). Occurrence probability ranges from 0 to 1, with a value of 1 indicative of a 100% occurrence

probability. Predicted biomass equates to grams per square meter of seafloor ($g.m^{-2}$). All models were constructed in R 3.2.0 with the package *randomForest* (Liaw & Wiener 2002).

Occurrence or biomass models for each vulnerable taxa included all 104 samples (observations) and 19 predictor variables. Swept area (log m^{-2}) was also included as an offset in the model to account for sampling intensity. Each model included 1,500 classification trees and I used a random subset of 67 % of the data without replacement to build single trees. I chose *m,* the number of variables randomly drawn at each split, to maximize classification accuracy.

For the occurrence models, accuracy was reported as the area under the receiver-operating characteristic curve (AUC). AUC ranges from 0 to 1, with values >0.9 indicating excellent accuracy, values between 0.7–0.9 considered as useful, and below 0.6 indicating a performance no better than random. AUC values were calculated using the package *PresenceAbsence* (Freeman & Moisen 2008) in R. For biomass models, accuracy was reported as the percent variance explained (R^2): R^2 =1– MSE_{OOB}/observed variance, where MSE_{OOB} is the mean square error (MSE) between observations and out-of-bag (OOB) predictions (average across all trees). Higher values of R^2 indicate better model performance. In addition, I calculated the correlation between observed and predicted values using point-biserial calculations for the occurrence data and Pearson's correlation coefficients for biomass to evaluate the bias and consistency of model predictions.

The importance of individual variables to prediction accuracy of vulnerable taxa was determined by how much worse the OOB predictions were with or without the help of that predictor. An increase of prediction error (MSE_{OOB}) indicated a higher contribution of that variable to the prediction accuracy. MSE_{OOB} and the accuracy importance measure (increase of MSE_{OOB}) were computed for each model/vulnerable taxa combination. I also plotted the partial dependence between each vulnerable taxa and key environmental predictors to evaluate the marginal effect of that variable on the occurrence probability or biomass.

Predictions of vulnerable taxa across HIMI were made on the original 9 km^2 grid (identical to the input variables) spanning the HIMI EEZ and depths between 150 to 1500 m. Predictions were limited to these depths due to the depth range of beam trawl samples (168 to 970 m). Environmental layers used as predictor variables are shown in Fig. 16. The predicted maps of occurrence and biomass are displayed in colour classes using Jenks Natural Breaks Optimization method to maximize the differences between the classes. Mapping used ESRI ArcGIS v10.1 and R package *sp* (Bivand *et al.* 2008).

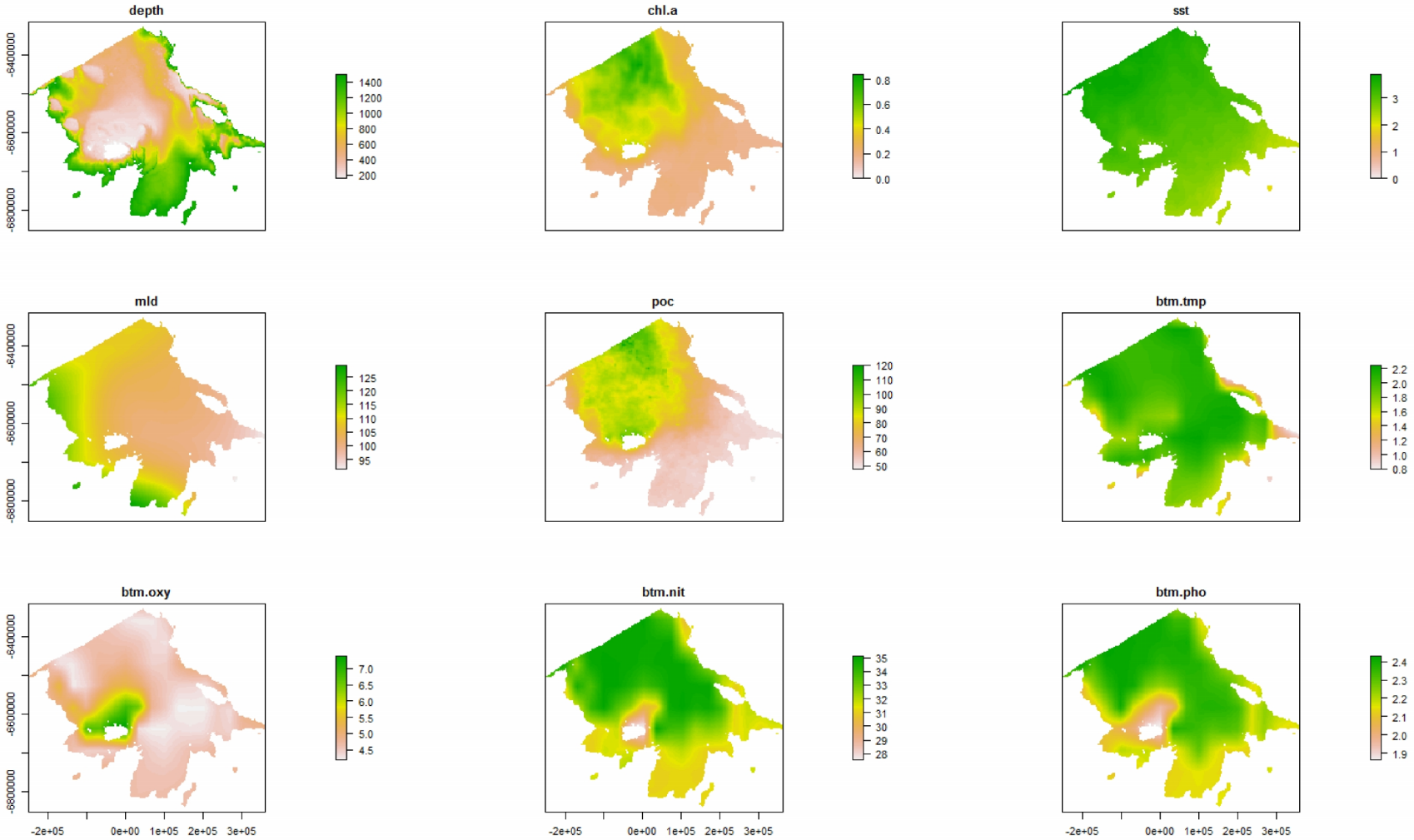

Fig. 16 Environmental data between 150 to 1500 m depth within the Heard Island and McDonald Islands (HIMI) Exclusive Economic Zone (EEZ). Data are standardised to a grid cell resolution of 9 km^2. Concentrations of nitrate, phosphate and silicate are in micromoles per litre ($\mu mol\ l^{-1}$) and bottom oxygen in millilitres per litre ($ml\ l^{-1}$).

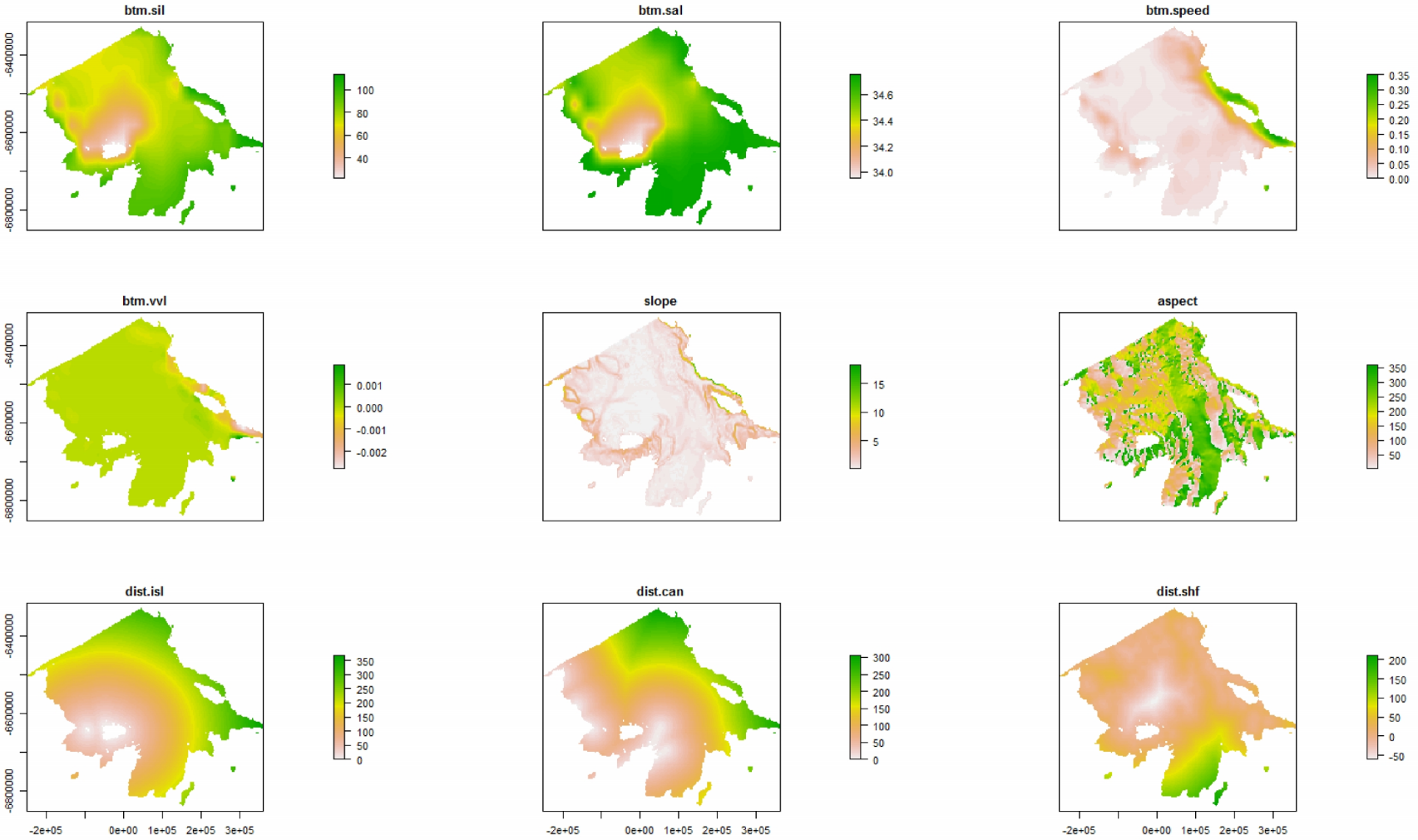

Fig. 16 (continued).

3.3.4 Identification of priority areas for conservation of vulnerable taxa

To identify priority areas for conservation of vulnerable taxa across HIMI, the predicted probabilities of occurrence and biomass were analysed using the spatial prioritization algorithm *Zonation* (Moilanen *et al.* 2005, Moilanen 2007), which has been used successfully in marine conservation planning applications (e.g. Leathwick *et al.* 2008). The *Zonation* algorithm ranks areas according to their priority for conservation. The ranking is achieved by evaluating raster layers for individual species and sequentially removing grid cells from the study area that, in the case of HIMI, have low predicted probabilities of occurrence and biomass, and thus the lowest conservation value. I used a simple core-area prioritization in Zonation 4.0 to guarantee the retention of high-quality areas identified for any particular vulnerable taxa. The algorithm first prioritised those cells with a high probability of occurrence (since predicted biomass was a function of the predicted probability of occurrence) and then selected for those cells with high values of predicted biomass. In other words, the algorithm sequentially considered the likelihood of an organism being present in an area and, if present, the likelihood it will occur at a higher biomass here than in other areas across HIMI. I ran the algorithm with weighted penalties according to model performance (AUC and R^2 values for each vulnerable taxa), meaning that more robust predictions were prioritised. I then compared the most important 15 % of the study area retained by the prioritisation algorithm to the existing MPA at HIMI. This 15% threshold was selected based on the Aichi Biodiversity Targets set by the Convention on Biological Diversity (CBD 2010). Target 11 calls for the conservation of 10% of all coastal and marine areas by 2020. Thus focus was given to the top 10% of conversation priority areas identified, with inclusion of a 5% margin to account for model error.

3.4 Results

3.4.1 Model performance

The RF occurrence models for all taxa provided an excellent discrimination between areas of presence and absence (AUC >0.87, Fig. 17a) and showed a high correlation between observed data and predicted probability of occurrence (r >0.9, Fig. 17b). Compared to the occurrence models, the performance of the RF biomass models was less accurate, but still explained 54 % to 78 % of the observed biomass variance (R^2) for vulnerable taxa (Fig. 17a), with strong correlations between observed and predicted biomass (Pearson's r >0.9, Fig. 17b). Linear trends in scatter plots (Fig. 18), suggests that the OOB predictions of biomass for all vulnerable taxa were on the proper scale with minor deviations from the observations.

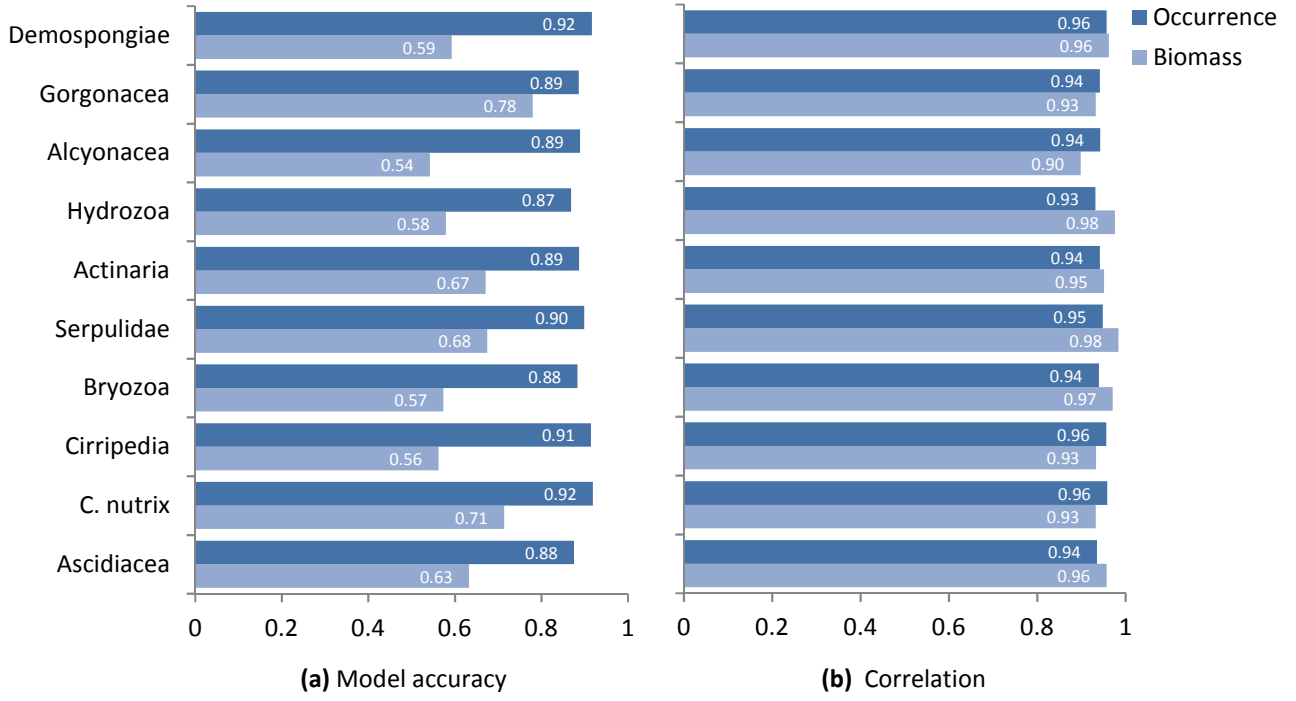

Fig. 17 Random Forests (RF) performance on discriminating the occurrence and biomass of vulnerable taxa. Performance was assessed on two metrics. **(a)** Model Accuracy reported as the area under the receiver-operating characteristic curve (AUC) for the occurrence models and percentage variance explained (R^2) for the biomass models. **(b)** Correlation between observed and predicted values was evaluated using point-biserial correlation values for the occurrence data and Pearson's correlation coefficients for biomass.

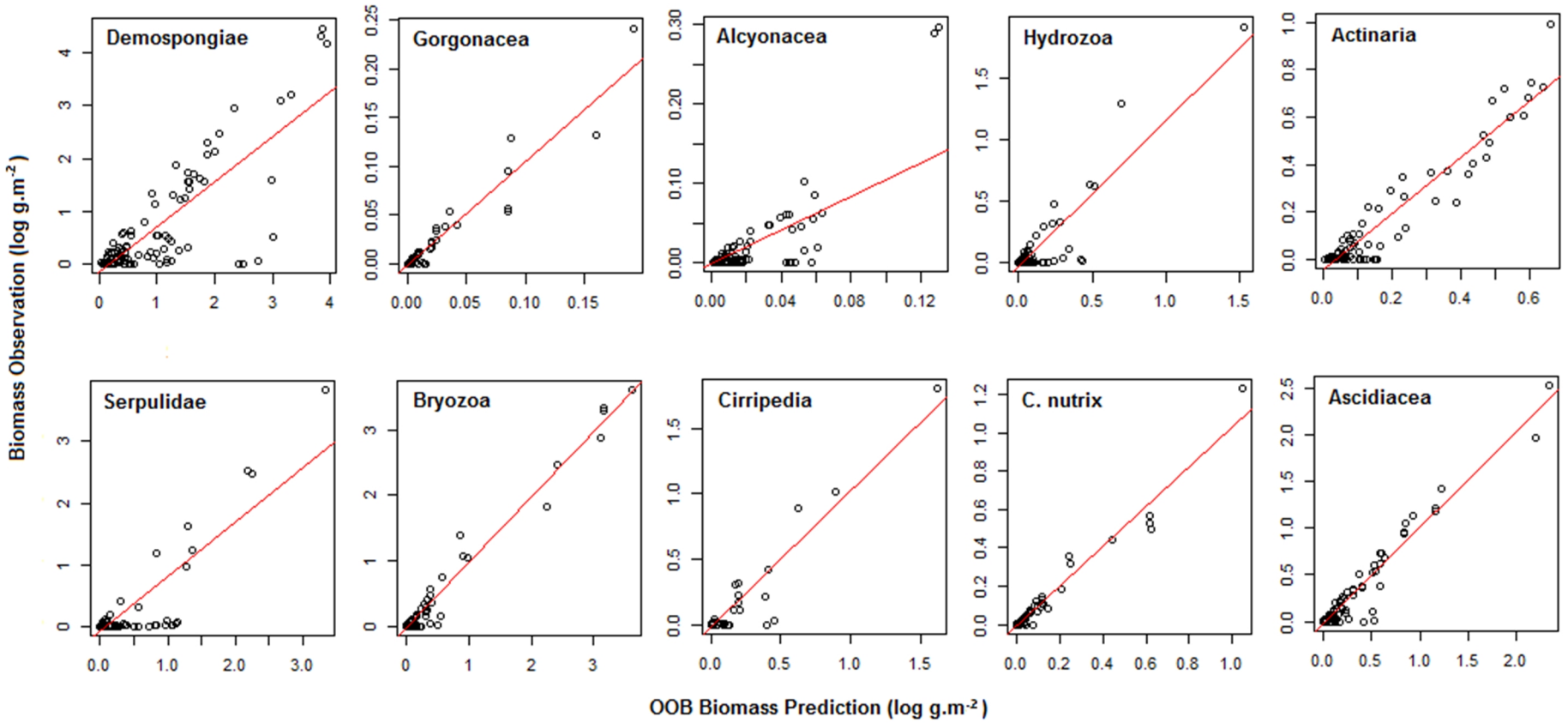

Fig. 18 Observed against out-of-bag (OOB) predicted biomass for RF models of vulnerable taxa. Regression line, in red, computed between observed and OOB predictions.

3.4.2 Environmental proxies for vulnerable taxa

Depth, distance to canyon and the concentration of particulate organic carbon (POC) were the most important variables for accurately predicting occurrence of vulnerable taxa (Fig. 19a). Depth was particularly important to Serpulidae and Demospongiae; distance to canyon to Ascidiacea and Actinaria; and POC to *Ctenocidaris nutrix* and Bryozoa. Also notable were the importance of slope to Cirripedia, and the concentration of seafloor phosphate, oxygen and silicate to Gorgonacea, Alcyonacea and Hydrozoa, respectively. Sea surface temperature, bottom phosphate and oxygen concentrations, seafloor current speed and depth were the most important for accurately predicting biomass with notable influence over Demospongiae, Serpulidae, Bryozoa and Ascidiacea (Fig. 19b). Occurrence probability for most vulnerable taxa decreased with increasing depth, decreasing POC concentration and distance to canyon, whilst the relationships between seafloor phosphate concentration and vulnerable taxa were highly variable (Fig. 20). Biomass generally decreased with increasing depth, but was positively correlated with warmer sea surface temperatures and higher concentrations of phosphate and oxygen.

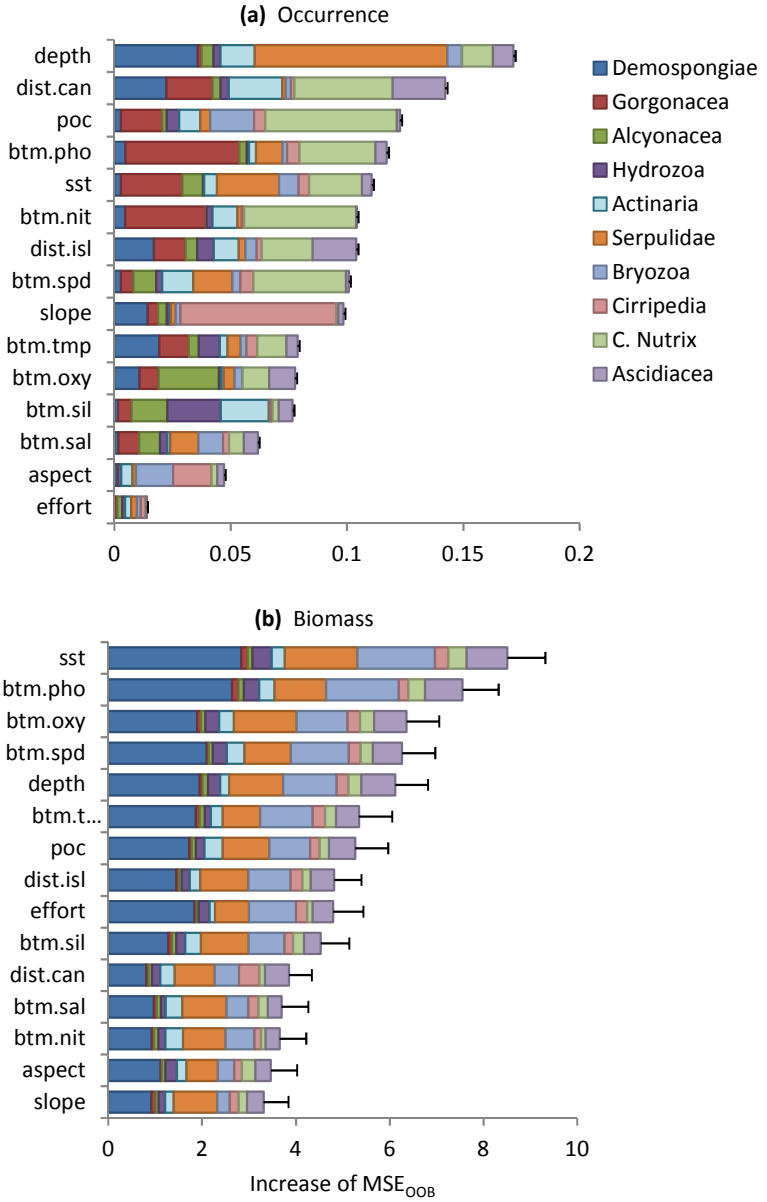

Fig. 19 Predictor importance on vulnerable taxa **(a)** occurrence and **(b)** biomass. The predictor importance of each vulnerable taxa was combined and mean standard deviation, SD (error bar), was calculated across all taxa for both RF models. Increase of mean square error (MSE_{OOB}) indicates the contribution to RF prediction accuracy for that variable. MSE_{OOB} values for biomass were fourth root transformed. Environmental variable abbreviations as per Table 14.

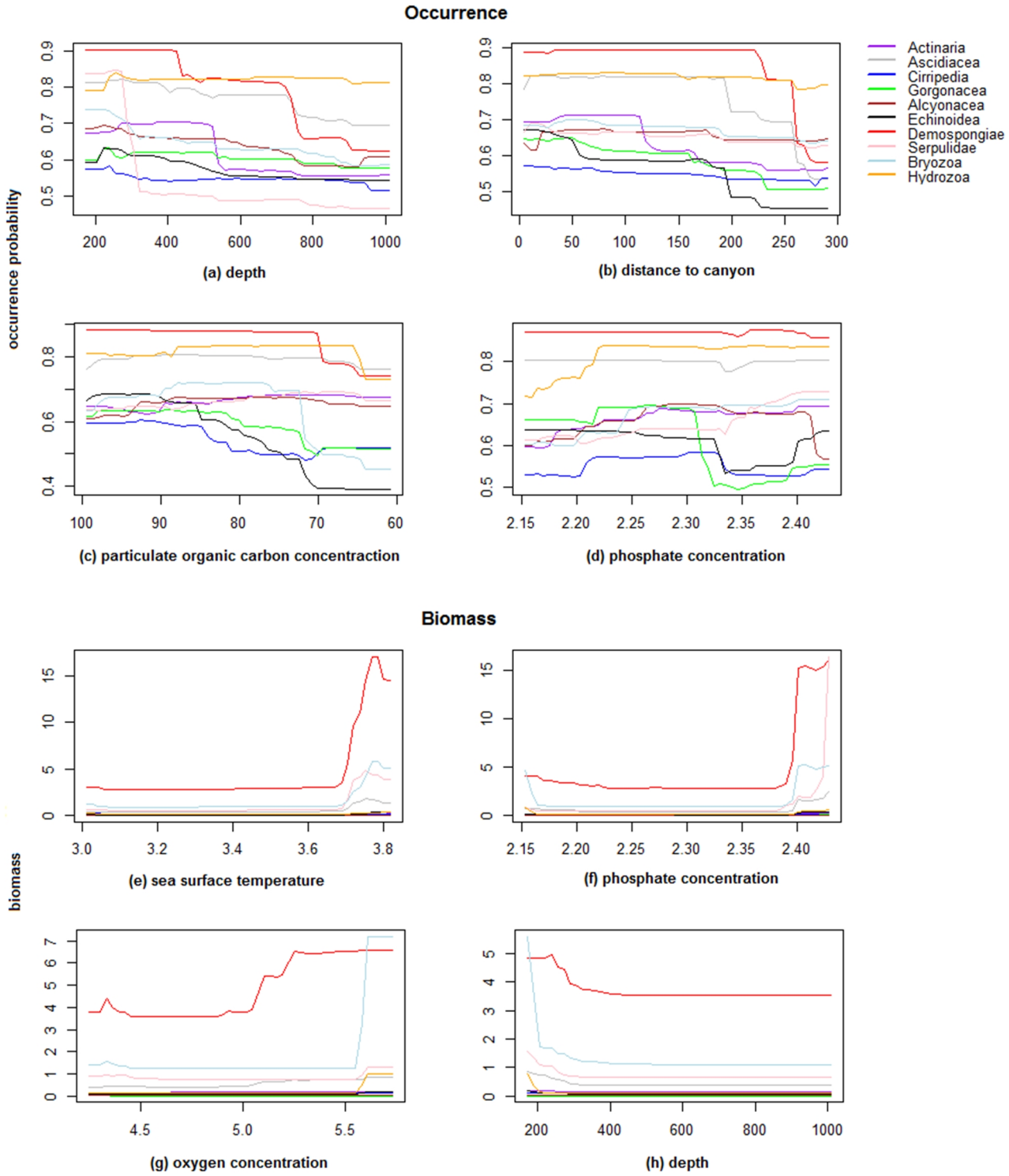

Fig. 20 Partial dependence plots between vulnerable taxa and environmental variables most influential on prediction accuracy (increase of MSE_{OOB}) for occurrence **(a** to **d)** and biomass **(e** to **h)**.

3.4.3 Patterns of predicted distribution and biomass

The spatial distribution and biomass of vulnerable taxa across HIMI was highly variable on a grid cell-by-grid cell basis (Fig. 21). Most importantly, a high probability of occurrence did not always coincide with a high biomass. For instance, the probability of Demospongiae occurring on Shell Bank and Pike Bank was high (>0.8), and yet estimates of biomass on Shell Bank were negligible compared with Pike Bank. This finding highlights the importance of considering both occurrence and biomass estimates in MPA planning.

For most taxa, the probability of occurrence was highest throughout the central plateau and on HIMI's banks and steeper slopes in waters above 500 m depth (Fig. 21). In the deeper waters most taxa were less likely to occur. Estimates of biomass displayed a similar trend, being particularly high on Pike Bank and across the central plateau, but lower elsewhere. Biomass for Demospongiae, Gorgonacea, Serpulidae, *C. nutrix* and Ascidiacea were all highest on Pike Bank and surrounding habitats. Alyconacea and Actinaria estimated biomass was highest near the islands and throughout the greater central plateau, with hotspots on Shell Bank and west of Pike Bank (Fig. 21). Hydrozoa, Bryozoa and Cirripedia were broadly distributed yet their biomasses were concentrated near the islands and in close surrounding waters.

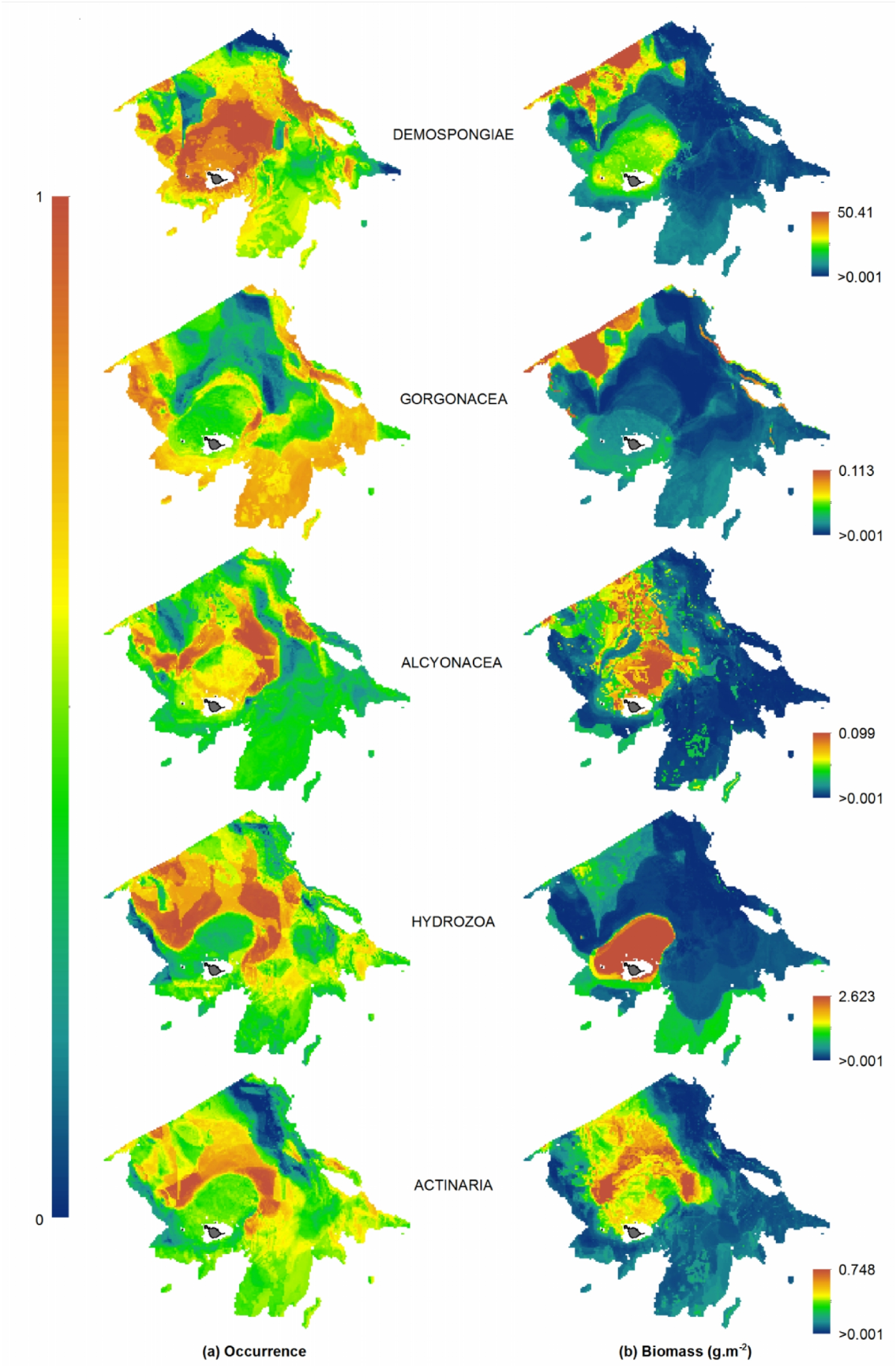

Fig. 21 Predicted **(a)** occurrence and **(b)** biomass of vulnerable taxa across HIMI between 150 and 1500 m depth. Left images show the probability of occurrence (0 to 1, where 1 = 100% occurrence probability) within a grid cell whilst images on the right show the likely biomass ($g.m^{-2}$) when present.

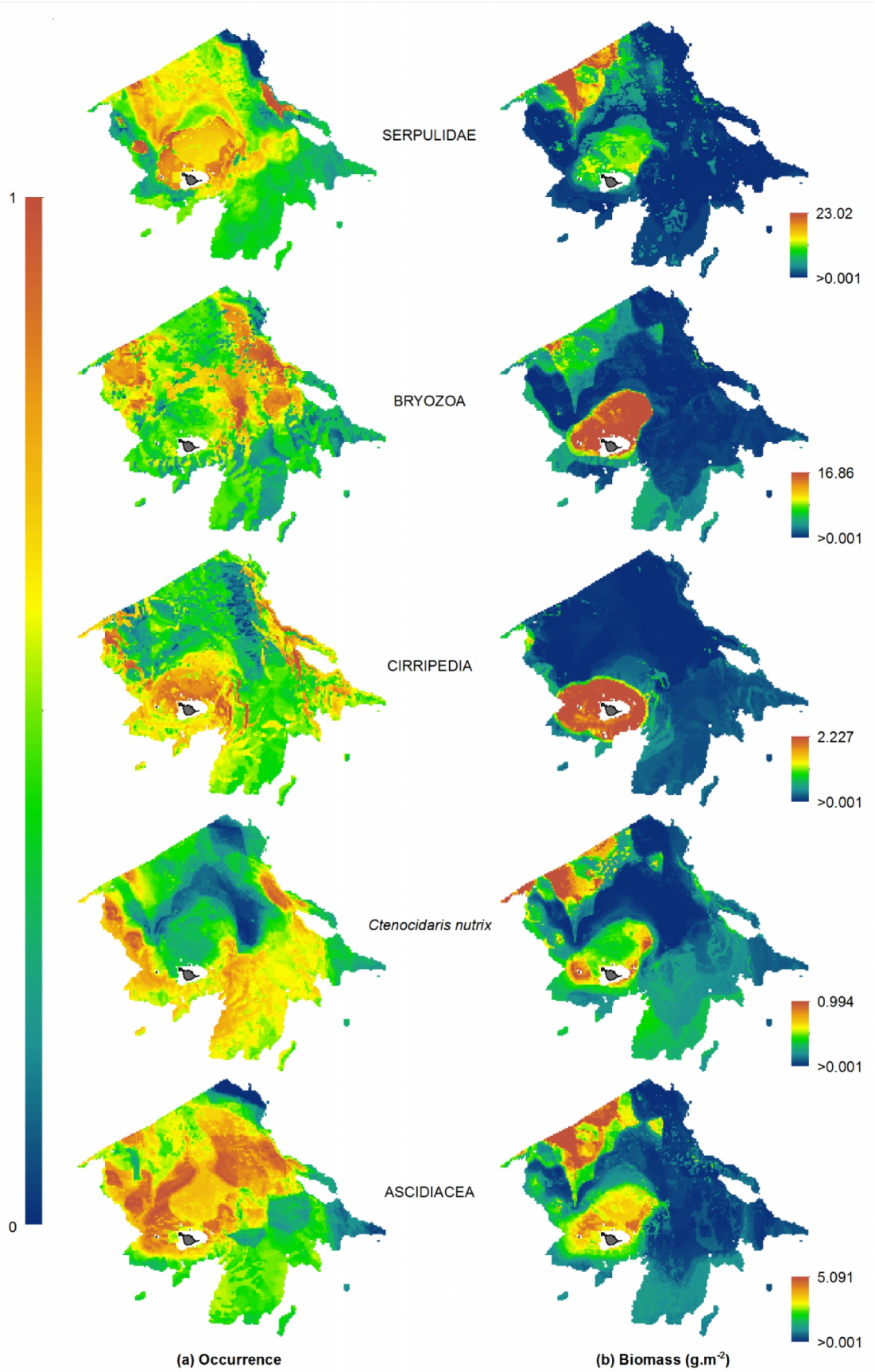
SERPULIDAE
BRYOZOA
CIRRIPEDIA
Ctenocidaris nutrix
ASCIDIACEA
1
0
23.02
>0.001
16.86
>0.001
2.227
>0.001
0.994
>0.001
5.091
>0.001
(a) Occurrence
(b) Biomass (g.m-2)

Fig. 21 (cont)

3.4.4 Priority areas for conservation of vulnerable taxa

The areas identified as highest conservation priority for vulnerable taxa included HIMI's banks/seamounts, central plateau margins (i.e. eastern and western margins of the central plateau), west and south-facing continental slopes, and shallow seascapes nearest the islands (Fig. 22). Aurora, Coral and Shell Banks were consistently retained in the most important 10% of the study area and are already protected by the HIMI MPA. Pike Bank was identified as an area of high conservation priority (top 2%) but falls outside the MPA. Similarly, high conservation areas on HIMI's central plateau and continental slope lie outside the existing MPA's boundaries. Nevertheless, more than a quarter of the top 2% and 5% conservation priority areas, and almost half of the top 10% and 15% areas, are currently represented within the MPA (Table 15).

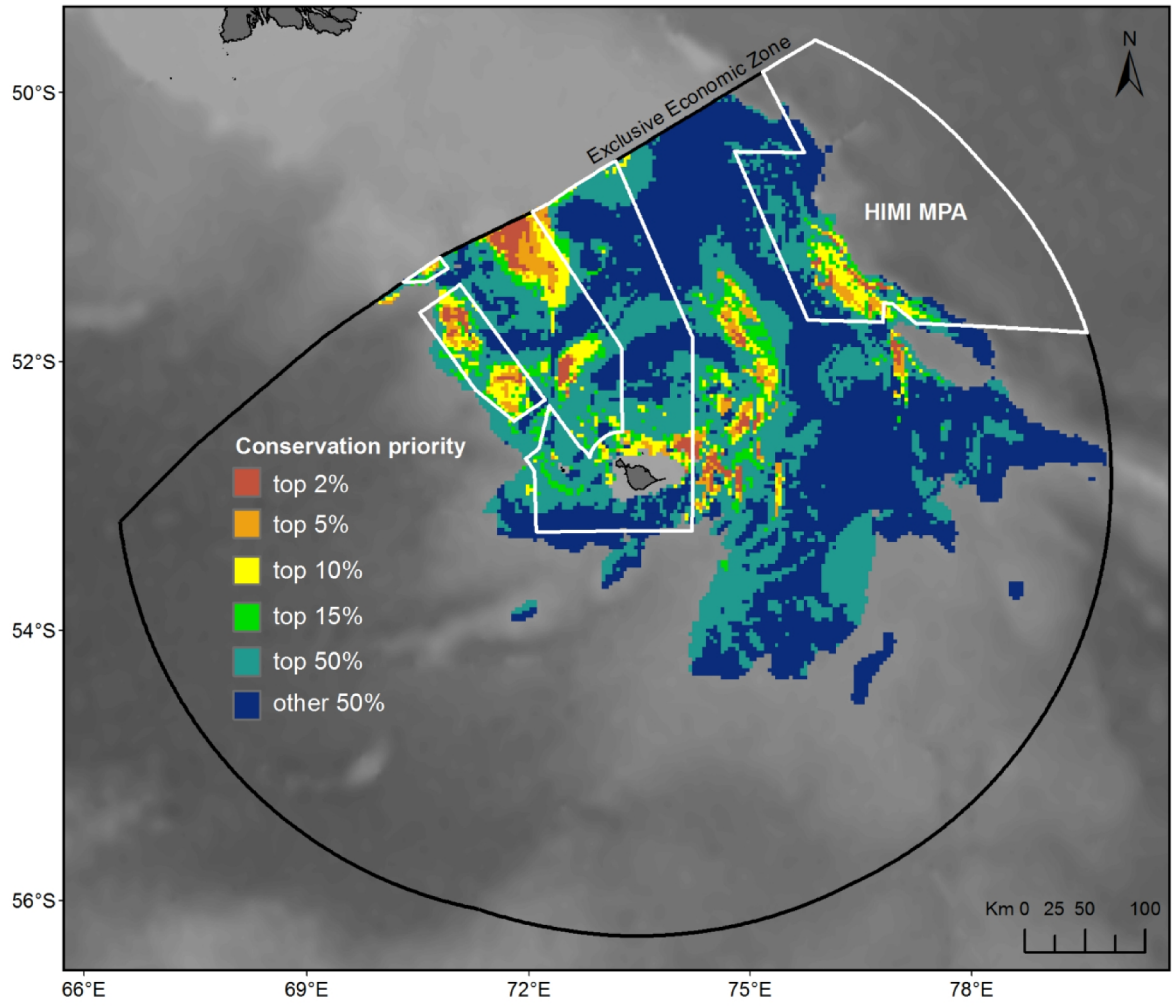

Fig. 22 Priority area for conservation of vulnerable taxa across HIMI between 150 to 1500 m depth identified using *Zonation*. The colour of shading reflects the priority for conservation (in % of total study area); red being the areas of greatest conservation significance. The white polygons denote the HIMI MPA.

Table 15 Summary of conservation priority areas represented within the HIMI MPA. Areas were identified using Zonation. Rasters included 15,288 3x3 km grid cells. Summary data include the number of grid cells inside and outside the MPA and their conservation priority.

	Grid cells		% Protected	
Conservation priority	*Inside MPA*	*Outside MPA*	*Inside MPA*	*Outside MPA*
top 2%	89	217	29.1	70.9
top 5%	168	291	36.6	63.4
top 10%	355	409	46.5	53.5
top 15%	310	454	40.6	59.4
other 85%	3302	9693	25.4	74.6

3.5 Discussion

HIMI's banks and areas of the central plateau and continental slope supported dense populations of vulnerable taxa (i.e. high occurrence and biomass), many of which are protected by the HIMI MPA. However, predictive models suggest the presence of considerably high conservation-value assemblages outside the MPA which may warrant further investigation. Predictions of the response of vulnerable taxa to environmental variables reported to influence patterns of megabenthos in the deep-sea agree with known patterns of occurrence and biomass in relation to depth, food availability and physical oceanography. All variables combined provided an excellent discrimination between areas of presences or absence, but were less accurate for biomass, indicating that additional parameterisation or validation through sampling is necessary to improve the model fit. Nonetheless the RF framework offered a similar and powerful tool for informing the spatial distribution of high conservation-value assemblages across HIMI and can be readily applied to other deep-sea areas where predictions are necessary to assist with resource management.

3.5.1 Environmental drivers of benthic biodiversity

The occurrence of most vulnerable taxa declined with increasing depth; a widely recognised pattern for the megabenthos (Denisenko *et al.* 2003, Jones *et al.* 2007, Smale 2008). Explaining this relationship is difficult since depth itself is not a driver, but rather a proxy for a suite of other parameters that change with depth such as food availability, temperature or oxygen concentration. Of the suite of depth-related parameters, food availability is generally considered to explain the trend, since the volume of food (i.e. particulate matter) reaching seafloor communities declines markedly with increasing depth (Rowe 1983, Gage & Tyler 1991). In this study, particulate organic carbon (POC) served as a proxy for food supply and was positively correlated to the occurrence of most vulnerable taxa. POC is a primary food source for benthic communities and is transported to the seafloor through sinking particulate matter (Turnewitsch *et al.* 2007). Hence a decreasing quantity and quality of sinking particulate matter (or POC) with increasing depth and distance from the islands' productive coastal waters may explain the decline in occurrence of vulnerable taxa with depth; a pattern which is clearly shown in these results (Fig. 21).

Distance to the nearest canyon axis was also an important proxy for occurrence of vulnerable taxa. Several underwater canyons exists across HIMI's southern and western slopes (O'Brien *et al.* 2009) and samples collected near these features contained the majority of vulnerable taxa assessed, and often at high biomasses. Underwater canyons have long been considered important habitats for marine life and have been observed to sustain enormous biomasses of benthos, particularly near the

canyon head (De Leo *et al.* 2010, Vetter *et al.* 2010). This abundance of life has been attributed to the complicated patterns of hydrography, flow and sediment transport and accumulation that can occur inside these features (Shepard *et al.* 1974, Oliveira *et al.* 2007, Garcia *et al.* 2008). For instance, conditions inside canyons, such as accelerated currents, can lead to increased particulate matter concentrations (Bosley *et al.* 2004, Genin 2004, Canals *et al.* 2006, Company *et al.* 2008) and thus enhanced benthic productivity, which in turn may impact recruitment and survival of benthic taxa. HIMI canyons are positioned such that they channel nutrient rich waters arriving from the eastward flowing ACC (van Wijk *et al.* 2010), and sinking particulate matter from the sea surface or productive coastal waters and therefore, may be expected to support higher densities of vulnerable taxa due to locally enhanced productivity. Another intriguing observation was the relationship between occurrence and phosphate concentration. In temperate ecosystems, phosphate is a limiting nutrient for aquatic organisms, particularly for algae, which can bloom under excess concentrations (Magnien *et al.* 2000, Burkholder *et al.* 2001, Glibert *et al.* 2001, Anderson *et al.* 2002). In the Southern Ocean however, phosphate is an abundant micronutrient which is more likely to promote primary production rather than limit it. Thus phosphate-promoted primary productivity maytranslate to a higher flux of particulate matter and sustenance of dense populations of benthic fauna. Nonetheless, the actual links between phosphate and diversity/abundance of vulnerable taxa in the Southern Ocean remain unclear.

Biomass also declined with increasing depth, but this decline was exponential and could be attributed largely to changes in SST and concentrations of dissolved oxygen (DO) and phosphate. For example, bryozoan biomass was high above approximately 500 m depth on Pike Bank and the central plateau, but decreased exponentially with increasing depth thereafter, suggesting a limiting factor around the 400 to 500 m depth zone.

Community changes with SST are often attributed to planktonic influences. Kirby *et al.* (2008) found that planktonic larval abundance for echinoderms, arthropods and molluscs in the North Sea was positively and immediately correlated to SST. Flow-on effects to benthic communities may include enhanced recruitment and food supply. High plankton levels leading to year round export of nutrients to the seafloor has been found to benefit the recruitment and growth of many benthic species in the North Sea (Morton 1983, Kirby *et al.* 2008). SSTs across the study area varied between 2.4 and 4.3°C, with the warmest waters recorded near Pike Bank due to its higher latitudinal position and the proximity to the Polar Front (PF) (Park *et al.* 1993), offering a feasible explanation for the high biomass of vulnerable taxa observed on the bank.

DO concentration was highest near the islands and throughout the central plateau (Fig. 16) where hydrozoans, bryozoans and cirripeds were abundant (Fig. 6). The actual DO requirements for these taxa and other deep-sea benthos are poorly known. Near-shore invertebrates of the East Coast of the United States have be observed to abandon areas when DO falls below 2.0 mg/l and exhibit reduced growth and survival rates below 1.0 mg/l (EPA 2000). In laboratory trails, cold-temperate demosponges have been shown to tolerate low oxygen concentrations (<2.0 mg/L), for brief periods (Gunda & Janapala 2009), whilst temperate corals need at least 4.0 mg/L to survive (Haas *et al.* 2014). At HIMI, DO concentration ranged between 4.0 and 7.5 ml/L (approximately 5.7 to 10.0 mg/L) suggesting that the above-mentioned taxa may prosper under higher DO concentrations, and that lower oxygen levels in the adjacent troughs (i.e. east and west of the central plateau) may be less favourable for vulnerable benthos.

Current speed was also important to biomass. The majority of vulnerable taxa assessed were sessile suspension-feeders which rely on currents for a supply of food (Starmans *et al.* 1999). Hence, areas of higher current velocities like HIMI's westerns banks and southern slopes, which intercept the eastward flowing ACC, are likely to provide more favourable feeding conditions for these taxa.

3.5.2 Protection of benthic biodiversity at HIMI

Analysis of predictions using *Zonation* highlighted HIMI's banks and numerous areas across the central plateau and continental slope as priority areas for conservation, many of which are currently protected by the MPA. However, additional high conservation value assemblages were also identified in unprotected waters which may warrant further investigation or conservation. Presently, 29% of the highest conservation priority areas (top 2%) for vulnerable taxa are encompassed within the HIMI MPA. This exceeds the conservation target of 10% set by the *Convention on Biological Diversity* in 2010 for protection of representative marine areas (Target 11, Decision X/2, Strategic Plan for Biodiversity 2011-2020), and almost meets the target of 30% set by the *International Union for the Conservation of Nature* (IUCN) at the World Parks Congress in November 2014. Hence, these predictive models suggest that the Australian government is well positioned to meet conservation targets in regard to vulnerable marine benthos and the HIMI MPA.

3.5.3 Prediction of biomass vs. presence

RF models provided an excellent discrimination between areas of presence and absence (AUC >0.87) and explained >54 % of the observed biomass variance (R^2) for vulnerable taxa. Given the relatively high intensity of sampling across HIMI's geomorphic types, including the banks and

shallow plateau, I have high confidence in the predictions of biomass in these areas that apparently support the highest biomass of vulnerable taxa. The deeper areas of the plateau are less well sampled, however they seem to support lower biomasses overall. These predictions do not, however, preclude the existence of locations where important aggregations of vulnerable taxa are present but were not sampled and, therefore, were unable to be predicted using the RF framework developed here. However, as the framework developed can readily assimilate new observations, targeted sampling of deeper geomorphs, such as the seamounts to the southeast of Shell Bank, would improve the robustness and generality of this study.

The environmental variables used in the model each contributed to prediction accuracy suggesting limited redundancy. In fact, these variables were particularly successful at discriminating between areas of presence or absence. However, the accuracy of the biomass models suggests that additional variables could significantly improve the model. For instance, substrate-type is often ascribed as a proxy of benthic biodiversity (McArthur *et al.* 2010) and if available/included in the model would most likely increase the variance explained. This assessment used annual means for remote sensing data as seasonal values were not available for some predictors (i.e. CARS data), but there is potential that finer temporal data, i.e. quarterly or biannual, may influence the predictions. Although where authors have incorporated seasonality, for example decadal mean and standard deviation of monthly values, a high correlation between them was observed (e.g. Wei *et al.* 2010), suggesting that difference among predictors, which are typically on very different scales, may mask correlations owing to seasonal variation. Notwithstanding, expanding the model by including environmental layers of high resolution in time and space could improve the model. At the scale of HIMI, fishing disturbance was a poor predictor of biomass. However, this may be due to the limited range of disturbances sampled. The highest level of disturbance to a station in this study was 2.6 km^2 but in some areas the area of seafloor impacted in a single 3 x 3 km cell is > 9 km^2 (i.e. the entire seafloor area within the cell is disturbed by bottom fishing) (Welsford *et al.* 2014b). Hence further sampling across a greater disturbance range might alter the predictor importance of fishing disturbance and improve model fit. Lastly, the focus of this study was physical surrogates and hence biotic surrogates were not considered. However, benthic communities are also influenced by biotic interactions and predation pressures (Freese *et al.* 1999, Halpern *et al.* 2008, McArthur *et al.* 2009) and hence integrating biotic predictors may also further strengthen the model.

3.5.4 Challenges and priorities for modelling seafloor ecosystems

Significant challenges still exist for spatial distribution modelling of deep-sea marine biodiversity where biota is out-of-sight and residing in environments that are constantly changing and extremely difficult to measure (Tremblay *et al.* 2009, Zipkin *et al.* 2010). The analyses presented here were complicated by factors such as habitat heterogeneity, applicability of sea surface variables to seafloor biota, taxonomic resolution and model selection. Benthic habitats are often highly heterogeneous resulting in patchy distributions of biota. Many recorded absences in the beam trawl data may therefore be considered false absences, e.g. the beam trawl traversed between two patches. Such methodological absences reduce the power of spatial distribution models (Martin *et al.* 2005, Lobo *et al.* 2010), and create uncertainty when models are evaluated. Many of the variables used here and in similar studies (e.g. Wei *et al.* 2010) are derived from the sea surface (e.g. remote sensing estimates of SST or Chlorophyll-*a* concentration). The relationship between these easily measured sea surface proxies and conditions at the seafloor that actually promote aggregations of benthos are poorly known. Hence there is a possibility that the relationships observed may be coincidental. In addition, I used broad taxonomic groups like Demospongiae to demonstrate the utility of the spatial modelling. Yet species within these broad taxonomic groups may respond differently to environmental conditions resulting in over- or under-estimates of distribution or density. Finally, the choice of modelling approach may also affect the results as different models can provide different predictions of the distribution of a species. A comparison of RF to BRT, GLM and GAM identified RF as the better method for analysing the HIMI data, but by no means can it be concluded that RF is best overal.

There may be no single best approach to these issues, and simulations would be useful to thoroughly test alternate models, and combinations of data aggregated at different spatial, temporal and taxonomic resolutions, to determine what is most reliable for benthos in the deep-sea. However, the only true measure of model accuracy would be to conduct targeted field surveys and sampling. Nonetheless given the immediacy of the issue of managing bottom fishing to prevent significant adverse interactions with vulnerable ecosystems, and the practical difficulties associated with obtaining empirical data from the deep-sea, surrogate predictions like those presented here offer the only practical means to make reasoned decisions about high seas resource management.

Chapter 4 - Patterns and predictions of vulnerable marine benthos across East Antarctica

4.1 Abstract

Designation of a representative system of marine protected areas (RSMPA) across East Antarctica requires an understanding on distribution of benthic habitats most at risk to potential threats, including bottom fishing and climate change. However empirical data is lacking, and our capacity to undertake extensive surveys to accurately determine the abundance and distribution of marine species in the deep Antarctic benthos in a realistic timeframe to inform MPA planning is minimal. Here I applied models developed for sub-Antarctic benthos and based on environmental surrogates to predict the distribution of vulnerable benthic taxa across East Antarctica. Quantitative sampling of benthos and the co-located attributes of the environment were used to parameterise these models for eight vulnerable taxa, all of which were sessile suspension-feeders like sponges and corals. These parameters were subsequently used to predict the occurrence and biomass of vulnerable taxa across East Antarctica within a Random Forest (RF) framework and to identify conservation priority areas using *Zonation* (i.e. hotspots). Estimates revealed a number of hot spots, namely the Prydz Bay region, but also Gunnerus Ridge, west of both Enderby Land and Casey Station and patches between Adelie Land and George V Land. Importantly, these hotspots were encompassed within the proposed RSMPA for East Antarctica offering protection for these habitats should marine protected areas be established. Sample size, model extent and data resolution were all potential sources of uncertainty in the model estimates. However, given the difficulties of collecting empirical data from the deep Antarctic, this study provides rigorous predictions of the distribution of benthos necessary to assist with managing biodiversity in the region.

4.2 Introduction

As bottom fisheries expand into Antarctic waters (Constable & Holt 2007, Bensch *et al.* 2009), and the impacts of climate change become more prevalent (IPCC 2007), so too does the urgency to describe biodiversity at risk from these potential threats. Bottom fishing has caused significant adverse impacts to the benthic habitat in many oceans, particularly to sessile benthos (see reviews by Lokkeborg 2005, Kaiser *et al.* 2006). Impacts range from fine-scale species or habitat destruction through to large scale shifts in entire ecosystems (Collie *et al.* 1997, Kaiser *et al.* 2006, Tillin *et al.* 2006). This can most easily be understood by considering the example of fragile, slow-growing deep-sea corals which are damaged or destroyed by bottom trawling (Roberts & Hirshfield 2004).

Impacts of climate change are less immediate and more difficult to ascertain, but have been implicated in declines in benthic biodiversity or density including mass coral deaths due to ocean warming and ocean acidification (Ateweberhana *et al.* 2013).

The risks of these threats to Antarctic benthos remain unclear (Fabry *et al.* 2008, Widdicombe & Spicer 2008). Fished habitats are considered to experience low levels of natural disturbance, typically because they are at depths beyond the influence of surface processes like iceberg scour which can impact the seafloor to as deep as 500 m (Barnes & Lien 1988, Dowdeswell *et al.* 1993, Gutt *et al.* 2011). Antarctic shelf assemblages are often dominated by sessile suspension-feeders like sponges and cold-waters corals (Arntz *et al.* 1994, Starmans *et al.* 1999, Clarke & Johnstone 2003). These sessile benthos are inherently vulnerable to damage or mortality upon an interaction with bottom fishing gear due to their morphology (e.g. emergent and brittle) and low recovery potential (i.e. slow-growing and long-lived) (Martin-Smith & Welsford 2014). Their sessile lifestyle may also result in such taxa being inherently vulnerable to climate change as their dispersal, recruitment and growth/nutrition is dependent on currents and stable environmental conditions which are likely to change according to future climate predictions (see reviews by Turner *et al.* 2009, Constable *et al.* 2014, Gutt *et al.* 2015). Moreover, the presumed slow growth rate, relatively low abundance, patchiness, and isolation of many Antarctic benthic species emphasize the particular vulnerability of the Antarctic benthos to bottom fishing disturbances or changing physical processes (e.g. Roberts & Hawkins 1999).

In response to the potential threats from fishing and climate change and requirements under Agenda 21 of the United Nations World Summit on Sustainable Development (2002), the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is currently considering the adoption of a Representative Systems of Marine Protected Areas (RSMPA) in East Antarctica (Fig. 23). The proposed RSMPA covers some 1.9 million square kilometres over seven separate areas,

including habitats that are vulnerable to disturbance and host important ecological processes, such as nursery areas for toothfish and krill, and foraging areas for marine mammals and penguins (Constable *et al.* 2010, AAD 2013).

In developing the RSMPA plan in East Antarctica, the distribution and hence representativeness of protection for benthic habitats and their biota within the RSMPA was inferred from physical variables. This was necessary as empirical data required to characterize these habitats were not available at the time (Constable *et al.* 2010), and are still not available. It was noted that the uniqueness of the area with respect to the benthos, including protection of representative taxa or assemblages, may require further consideration to determine whether an appropriate level of protection is provided (Constable *et al.* 2010).

In this study, I applied methods developed in Chapters 2 and 3 to model and predict the distribution and biomass of benthos across East Antarctica, encompassing the RSMPA. Estimates focused on those taxa considered most vulnerable to disturbance from bottom-fishing gears including sponges and corals. To achieve this, the study had three primary objectives: (1) to sample benthic habitats to document vulnerable taxa in key deep sea locations in East Antarctica, (2) describe how observed patterns of biodiversity relate to physical parameters in these locations, and (3) to use the observed relationships to predict the distribution and biomass across the entire deep shelf of East Antarctica so that areas likely to contain vulnerable assemblages can be identified and incorporated into management plans.

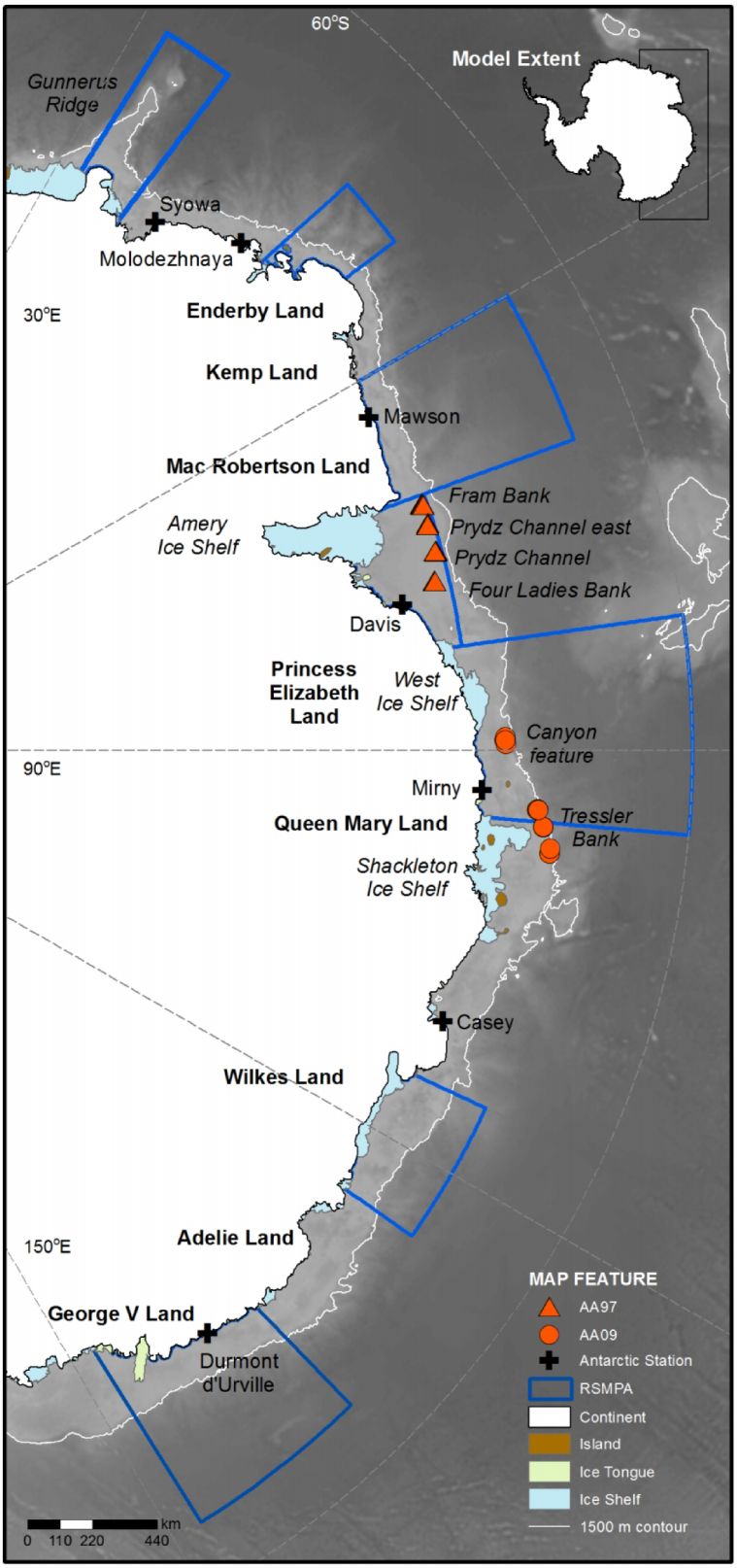

Fig. 23 Study area across East Antarctic including benthic survey stations for two research surveys aboard the research vessel *Aurora Australis* (AA), AA97 and AA09.

4.3 Methods

4.3.1 Study area

The area of interest encompassed the continental shelf/slope of East Antarctica between 30° to 150°E and outwards from the coast to 60°S (Fig. 23). This area includes the proposed RSMPA and CCAMLR Divisions 58.4.1 and 58.4.2, although it excludes the northern most section of Division 58.4.1, as this area is part of the Greater Kerguelen Plateau province, which is considered biogeographically distinct from East Antarctica. CCAMLR manages an exploratory longline fishery for toothfish throughout these divisions and illegal fishing using demersal longlines and gillnets has been reported (Lack 2008, Österblom *et al.* 2015). This study focused on depths between 150 to 1500 m to encompass depths typically targeted by the fishery (CCAMLR 2015) and the extent of available datasets.

4.3.2 Benthic data

Empirical data on benthic species distribution and abundance in East Antarctica were collated from two surveys aboard the research vessel *Aurora Australis* (AA). The first, AA97, was conducted in February and March 1997 and the second, AA09, in December 2009 and January 2010. Data for AA97 were collected from 19 stations belonging to four broad localities; Fram Bank, Prydz Channel, east of Prydz Channel and Four Ladies Bank. AA09 sampled 15 stations belonging to two localities, the shelf break of Tressler Bank adjacent to the Shackleton Ice Shelf and a canyon feature on the continental shelf between Drygalski Island and the West Ice Shelf. The purpose of these surveys was to provide better understanding of the marine ecosystem in the region and factors influencing the distribution of Antarctic benthic invertebrates. AA09 also aimed at targeting areas of particular interest to fisheries. Sampling across the two voyages covered a total of 41,040 m^2 of the sea floor at depths between 300-1157 m (Table 16).

The benthos at each station was sampled using a research beam trawl equipped with a 10 mm cod-end liner. Benthos retained in the trawl belonged mostly to the mega-epibethos, meaning those animals >10 mm in length living on or near the seafloor surface. The trawl was deployed for up to 15 minutes, and towed at a speed of 1 to 1.5 knots. Swept area, i.e. the area of seafloor sampled by each trawl, was determined by multiplying trawl distance by the beam trawl width (2.7 m). Trawl distance was calculated as the great circle distance from the start and finish coordinates, which were determined from line tension and vessel position. All material recovered from the net was sieved over a 10 mm mesh, sorted, weighed and preserved in media appropriate for each taxonomic group (crustaceans – formalin, other taxa – 70% ethanol) at the time of sampling. Organisms were sorted

based on gross morphological differences into species or taxonomic groups likely to represent species (*sensu* 'operational taxonomic unit' (OTU) (Butler *et al.* 2000b) or 'putative taxon' (Ward *et al.* 2006a). Unsortable residual material, usually composed of broken Porifera and Bryozoa, was weighed and sub-sampled. Subsamples were retained for thorough examination in laboratory conditions. The weight (grams) and number of individual specimens (non-colonial only) for each taxon was recorded for each sample. Counts and weights were standardised to abundance and biomass per square metre of the seafloor ($n.m^{-2}$ and $g.m^{-2}$, respectively) using swept area.

Table 16 Haul details for stations sampled during cruises AA97 (1997) and AA09 (2009). Latitude, longitude and depth are the midpoint for each beam trawl track. Depth was obtained from GEBCO 2008.

Area	Cruise/Station	Latitude	Longitude	Swept area (m^2)	Depth (m)
Prydz Channel East	AA97-09	-67.17	72.24	2160.27	540
	AA97-10	-67.18	72.23	1501.98	546
	AA97-11	-67.19	72.3	1412.25	544
	AA97-12	-67.2	72.36	1353.74	552
Fram Bank	AA97-16	-67.14	70.65	785.47	293
	AA97-17	-67.17	70.66	527.54	290
	AA97-18	-67.18	70.73	484.42	300
	AA97-19	-67.16	70.77	590.73	304
	AA97-20	-67.13	70.78	674.74	362
Prydz Channel	AA97-21	-67.17	74.47	806.13	428
	AA97-22	-67.16	74.42	979.15	437
	AA97-23	-67.19	74.42	586.24	440
	AA97-24	-67.21	74.47	821.7	440
	AA97-25	-67.2	74.51	631.8	436
Four Ladies Bank	AA97-26	-67.44	76.65	1107.12	320
	AA97-27	-67.45	76.71	783.08	320
	AA97-28	-67.45	76.68	884.7	316
	AA97-29	-67.45	76.69	381.15	312
	AA97-30	-67.45	76.71	306.54	317
Tressler Bank	AA09-06	-64.28	96.73	1394.9	1076
	AA09-08	-64.28	97.11	1544.4	707
	AA09-10	-64.28	97.1	846.9	833
	AA09-11	-64.29	97.12	1644	662
	AA09-14	-64.56	95.36	1793.5	562
	AA09-17	-64.56	95.32	1096	758
	AA09-18	-64.56	95.32	1644	701
	AA09-20	-64.8	94.18	1942.9	442
	AA09-21	-64.77	94.17	2192	1157
	AA09-22	-64.79	94.15	2142.2	699
Canyon feature	AA09-24	-65.86	89.29	2391.3	728
	AA09-25	-65.87	89.27	2590.6	522
	AA09-26	-65.87	89.29	1942.9	404
	AA09-29	-65.87	89.03	498.2	547
	AA09-30	-65.84	89.54	597.8	527

A review of the East Antarctic benthic biodiversity data identified 8 vulnerable taxa, all of which were sessile, suspension-feeding invertebrates (Table 17). Data for each vulnerable taxa were collated at a high taxonomic resolution to align with those taxonomic groups identified by CCAMLR as indicators of vulnerable marine ecosystems (VMEs) in the Southern Ocean (SC-CAMLR 2009, 2012).

Table 17 List of vulnerable taxa assessed for East Antarctica. 'Presence' is the number of beam trawl events out of 34 in which they were captured. Biomass is $g.m^{-2}$ and includes the range of observed values in parentheses (minimum to maximum).

Vulnerable taxon	Common name	Presence	Average biomass (min – max)
Porifera	sponges	33	17.52 (0.008 - 86.449)
Actinaria	anemones	18	0.564 (0.002 - 1.813)
Gorgonacea	horny corals or gorgonians	28	0.198 (0.001 - 1.157)
Hydrozoa	hydroids or sea ferns	18	0.335 (0.002 - 2.474)
Scleractinia	hard corals	18	0.059 (<0.001 - 0.162)
Pennatulacea	sea pens	17	0.034 (0.002 - 0.122)
Brachiopoda	lamp shells	20	0.011 (<0.001 - 0.034)
Ascidiacea	sea squirts	30	2.434 (0.002 - 30.519)

4.3.3 Environmental data

The analyses use synoptic data (generally remote sensed or modelled data) for 22 environmental variables to predict patterns of distribution and abundance of vulnerable taxa at an approximate finest-scale area of 0.1-degree (ca. ≈ 48.5 km^2 at 67°S). The environmental variables were grouped into six predictor categories (Table 18): (a) seasonal sea ice cover and variability, (b) sea surface properties relating to phytoplankton productivity including particulate organic carbon (POC) concentration, the major food supply to benthic communities (Vinogradov & Tseitlin 1983), (c) bottom water properties characterising seafloor habitats, (d) physical properties relating to seabed structure and relief, (e) distance as a proxy to point source influences (i.e. kilometres to the nearest canyon or the Antarctic coast) and (f) water depth. All synoptic layers were reclassified to a consistent 0.1-degree grid using bilinear interpolation for analysis and prediction. The extent of these analyses was restricted by the chlorophyll-*a* and POC climatology data, which had incomplete coverage in near-coastal regions due to sea ice cover, but were desired in the model since they are either known or suspected to be correlated with the spatial distribution and density of sessile benthos (McArthur *et al.* 2009, Wei *et al.* 2010). Values for all parameters were extracted from the grid cell containing the midpoint (latitude/longitude) of each beam trawl track. All layers were compiled and assessed in the software package ESRI ArcGIS v10.1 and R 3.2.0 (R Development Core Team 2010).

Table 18 Datasets of environmental predictor variables across East Antarctica. Data were interpolated from their original resolutions to a consistent 0.1-degree grid using bilinear interpolation based on layers derived by the Australian Antarctic Data Centre (AADC).

Variable	Short	Unit	Variable layer description	Reference
(a) Sea ice				
Sea ice cover	seaice	%	Proportion of time the ocean is covered by sea ice of concentration 85% or higher. Data based on AMSR-E satellite estimates of daily sea ice concentration at 6.25 km resolution.	Spreen *et al.* (2008)
Sea ice summer variability	seaice.var		Variability of sea ice cover during summer months. Data based on AMSR-E satellite estimates of daily sea ice concentration at 6.25 km resolution. The values given here are averaged over the 2002/03 to 2009/10 austral summer seasons.	
(b) Surface water				
Chlorophyll-*a*	chl.a	mg m^{-3}	Average of annual values from the MODIS (Moderate Resolution Imaging Spectroradiometer) aqua mission data from 2002/03 to 2009/10 austral summer seasons. Data interpolated from original 9 km grid resolution.	Feldman and McClain (2010)
Sea surface temperature	sst	°C		
Mixed layer depth	mld	m	Annual mean concentration derived from the CSIRO Atlas of Regional Seas (CARS 2009).	Condie and Dunn (2006)
Particulate organic carbon	poc	mg m^{-3}	Average of annual values from the MODIS aqua mission data from July 2002 to December 2009.	Stramski *et al.* (2008)
Annual light budget	light.bug		Annual light budget (cumulative solar radiation) reaching the water surface. Daily incident solar radiation was modelled assuming a cloud-free sky (Suri and Hofierka 2004). Sea ice data (AMSR-E sea ice concentration) were used as a mask: if sea ice was present on a given day then the solar radiation reaching the ocean surface was assumed to be zero. The annual light budget for a given pixel was therefore calculated as the sum of daily solar radiation values on all days when sea ice was not present. The values used are the mean annual light budget over the 2002/03 to 2010/11 austral summer seasons (1-Jul to 30-Jun). Calculations were made on the AMSR-E 6.25km polar stereographic grid, and then interpolated to the 0.1-degree rectangular grid using triangle-based linear interpolation.	Suri and Hofierka (2004), Clark *et al.* (2013)
(c) Bottom water				
Temperature	btm.tmp	°C	Annual mean concentration derived from CARS 2009. Data interpolated from original 0.5° grids.	Ridgway *et al.* (2002)
Dissolved oxygen	btm.oxy	µmol l^{-1}		
Nitrate	btm.nit	µmol l^{-1}		
Phosphate	btm.pho	µmol l^{-2}		
Silicate	btm.sil	µmol l^{-1}		
Salinity	btm.sal	PPS		
(d) Physical metrics				
Seafloor current speed	btm.spd	m s^{-1}	Current speed near the seafloor averaged over 12 snapshots from the CAISOM ocean model.	Galton-Fenzi *et al.* (2012)
Seafloor slope	slope	degree	Slope of the sea floor, derived from Smith and Sandwell V13.1 and ETOPO1 bathymetry data. Slope calculated on 0.1° gridded depth data using the equation given by (Burrough & McDonell 1998)	Burrough and McDonell (1998), Smith and Sandwell (1997)

Table 18 continued.

Variable	Short	Unit	Variable layer description	Reference
(e) Distance metrics				
Distance to Antarctica	dist.ant	km	Distance to nearest part of the Antarctic continent. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km.	AADC
Distance to canyon axis	dist.can	km	Distances to nearest canyon axis calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from Geoscience Australia's seafloor geomorphology data.	O'Brien *et al.* (2009)
Distance to maximum winter sea ice extent	max.ice	km	Mean maximum winter sea ice extent was derived from daily estimates of sea ice concentration from the National Snow and Ice Data Center (NSIDC). The closest distance of each grid point to this extent line was calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km.	Cavalieri *et al.* (1996, updated 2008)
Distance to polynya	dist.polyn	km	Distance to the nearest polynya area based on AMSR-E satellite estimates of daily sea ice concentration at 6.25 km resolution (see above). Pixels which were (on average) covered by sea ice for less than 35% of the year were identified. The distance from each grid point on the 0.1-degree grid to the nearest such polynya pixel was calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km. The threshold of 35% was chosen to give a good empirical match to the polynya locations identified by Arrigo and van Dijken (2003), although the results were not particularly sensitive to the choice of threshold.	Arrigo and van Dijken (2003)
Distance to shelf break	dist.shf	km	Distance to nearest area of sea floor of depth 500 m or less. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km from ETOPO1 bathymetry data.	Smith and Sandwell (1997)
Distance to upper slope	dist.upslp	km	Distance to the "upper slope" geomorphic feature from the Geoscience Australia geomorphology data set. Distances calculated in km using the Haversine formula on a spherical earth of radius 6378.137 km. Points inside of an "upper slope" polygon were assigned negative distances.	O'Brien *et al.* (2009)
(f) Water depth				
Depth	depth	m	Depth estimated from the General Bathymetric Chart of the Oceans (GEBCO) 0.1° grid bathymetric data series (GEBCO_08).	GEBCO_08 (2008)

4.3.4 Model construction, evaluation and prediction

The study uses the model framework developed in Chapters 2 and 3 to model and predict the occurrence and biomass of 8 vulnerable taxa across East Antarctica. The framework constructed in R 3.2.0 (R Development Core Team 2010) using the *randomForest* package (Liaw & Wiener 2002) consists of two sequential Random Forest (RF) models, one to predict the occurrence probability of each vulnerable taxa (termed 'occurrence model'), and one to predict the biomass of that vulnerable taxa given their presence in an area (termed 'biomass model'). Occurrence probability ranges from 0 to 1, with a value of 1 indicative of a 100% occurrence probability. Predicted biomass equates to grams per square meter of seafloor ($g.m^{-2}$).

Models for each vulnerable taxa included data from 34 observations (sampling stations) and 22 predictor variables. Biomass was logarithm transformed before conducting RF analysis and swept area ($\log m^{-2}$) was included as an offset in the model to account for sampling intensity. Models were built on 1,500 classification trees and used a random subset of 67% of the data without replacement to build single trees. I chose *m,* the number of variables randomly drawn at each split, to maximize classification accuracy.

For the occurrence models, accuracy was reported as the area under the receiver-operating characteristic curve (AUC). AUC ranges from 0 to 1, with values >0.9 indicating excellent accuracy, values between 0.7–0.9 considered useful, and values below 0.6 indicating a performance no better than random. AUC values were calculated using the package *PresenceAbsence* (Freeman & Moisen 2008) in R 3.2.0. For biomass models, accuracy was reported as the percent variance explained (R^2): R^2 =1–MSE_{OOB}/observed variance, where MSE_{OOB} is the mean square error (MSE) between observations and out-of-bag (OOB) predictions (average across all trees). Higher values of R^2 indicate better model performance. In addition, I calculated the correlation between observed and predicted values using point-biserial calculations for the occurrence data and Pearson's correlation coefficients for biomass.

The importance of individual variables to prediction accuracy of vulnerable taxa was determined by how much worse the OOB predictions were with or without the help of that predictor. An increase of prediction error (MSE_{OOB}) indicated a higher contribution of that variable to the prediction accuracy. MSE_{OOB} and the accuracy importance measure (increase of MSE_{OOB}) were computed for each model/vulnerable taxa combination and then visualized using Cleveland dot plots. Increase of MSE_{OOB} values were also ranked and plotted as histograms to assist with an interpretation of overall predictor variable importance across all model/vulnerable taxa combinations.

Predictions across East Antarctica were made on the original 0.1-degree grid (identical to the input variables) spanning 30°E–150°E, 70°S–60°S, and depths between 150 m–1500 m. Predictions were made of log biomass data. For interpretation, predicted mean biomass values were back transformed to median biomass values using exp(x). The predicted maps of occurrence and biomass are displayed in colour classes using Jenks Natural Breaks Optimization method to maximize the differences between the classes. Mapping used ESRI ArcGIS v10.1 and R package *sp* (Pebesma & Bivand 2005, Bivand *et al.* 2013b).

4.3.5 Identification of priority areas for conservation of vulnerable taxa

To identify priority areas for conservation of vulnerable taxa in East Antarctica, the predicted probabilities of occurrence and biomass were analysed in the spatial prioritization algorithm *Zonation* (Moilanen *et al.* 2005, Moilanen 2007), which has been used successfully in marine conservation planning applications (e.g. Leathwick *et al.* 2008). The *Zonation* algorithm ranks areas according to their priority for conservation. The ranking is achieved by evaluating raster layers for individual species (vulnerable taxa) and sequentially removing grid cells from the study area that, in the case of East Antarctica, have low predicted probabilities of occurrence or biomass, and thus the lowest conservation value. I used a simple core-area prioritization in Zonation 4.0 to guarantee the retention of high-quality areas identified for any particular vulnerable taxa.

4.4 Results

4.4.1 Model performance

The occurrence models for all vulnerable taxa provided an excellent discrimination between areas of presence and absence (AUC >0.95, Fig. 24a) and showed a high correlation between observed data and predicted probability of occurrence (Correlation >0.7, Fig. 24b). The biomass models also performed well, explaining more than 67% of the observed biomass variance (R^2) for vulnerable taxa (Fig. 24a). Strong correlations between observed and predicted biomass values were also observed (Pearson's *r* >0.82, Fig. 24b), as evidenced by generally linear trends in scatter plots for each taxa (Fig. 25). This suggests that the OOB predictions for all vulnerable taxa were largely unbiased, with minor deviations from the observations and a tendency to over-estimate biomass were zero values were observed (Fig. 25).

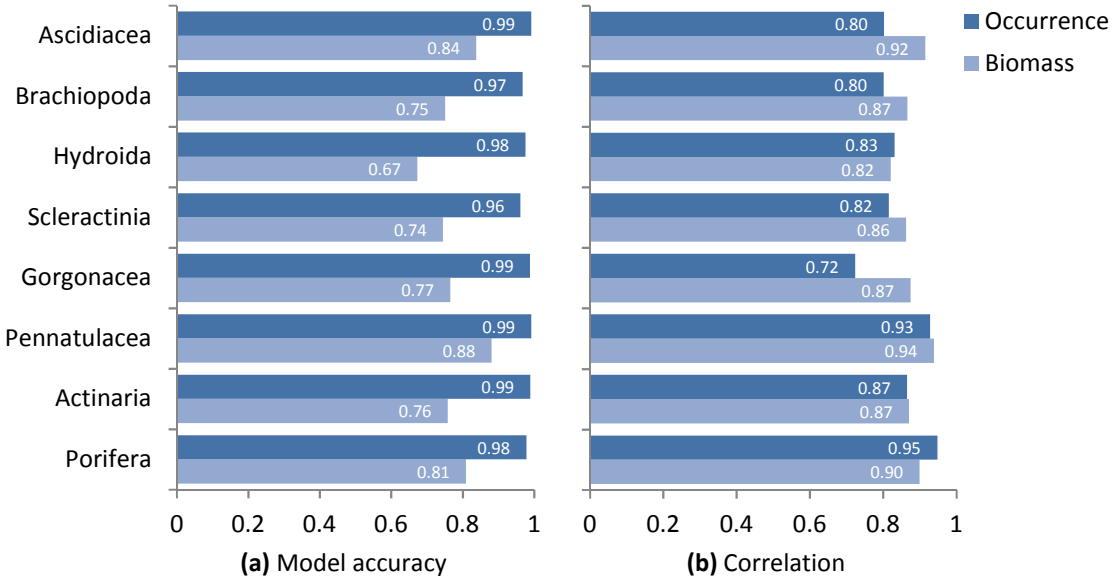

Fig. 24 Random Forests (RF) performance on discriminating the occurrence and biomass of vulnerable taxa. Performance was assessed on two metrics. **(a)** Model Accuracy reported as the area under the receiver-operating characteristic curve (AUC) for the occurrence models and percentage variance explained (R^2) for the biomass models. **(b)** Correlation between observed and predicted values was evaluated using point-biserial correlation values for the occurrence data and Pearson's correlation coefficients for biomass.

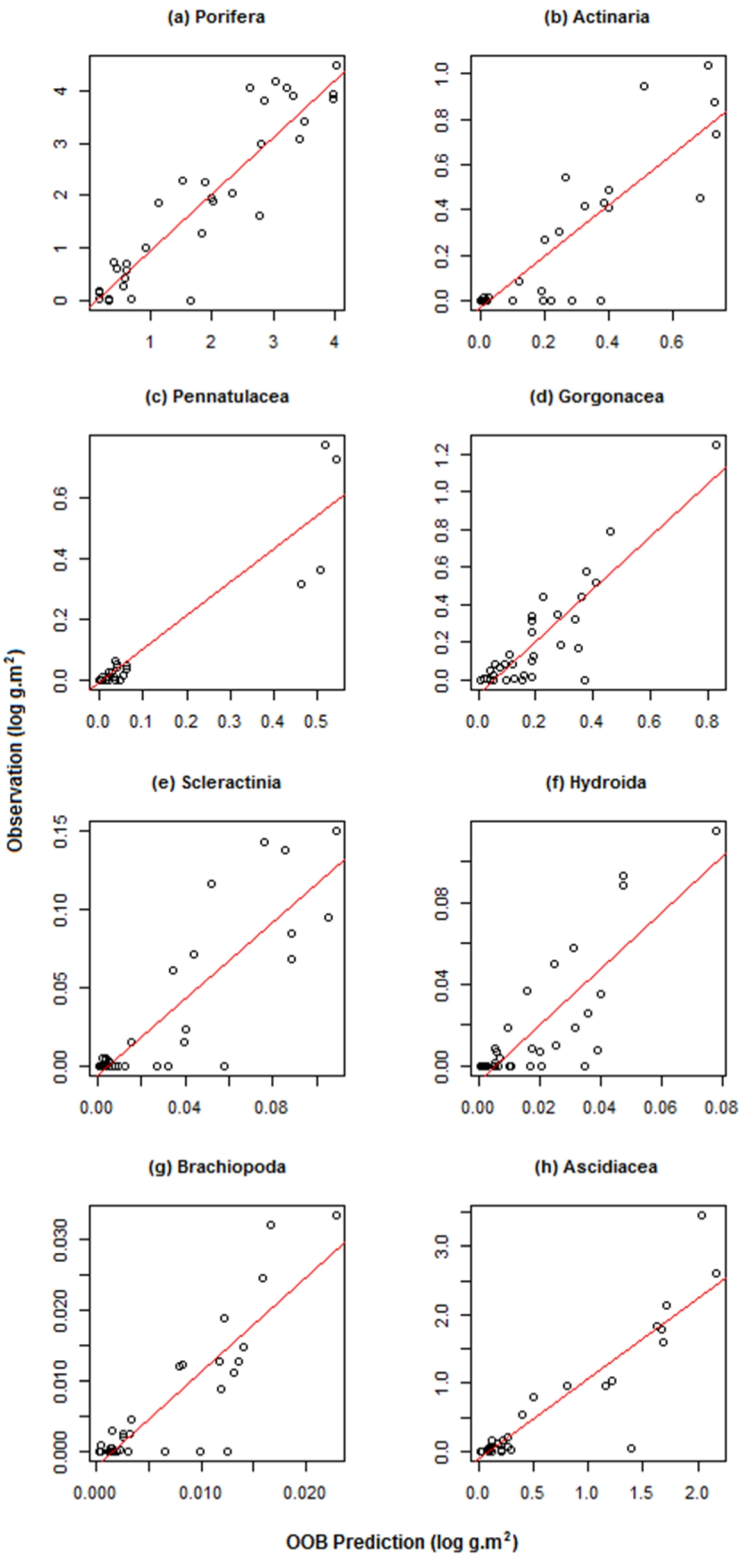

Fig. 25 Observed against out-of-bag (OOB) predicted biomass for RF models of vulnerable taxa present across East Antarctica. Regression line, in red, computed between observed and OOB predictions of log biomass (log g.m^{-2}).

4.4.2 Environmental proxies for vulnerable taxa

Overall, the most important variables for accurate predictions of occurrence were distance to the nearest canyon or area of Antarctic coast, and depth (Fig. 26a). Distance to the nearest canyon was particularly important to the occurrence of Pennatulacea, Scleractinians and Hydroids; distance to the Antarctic coast to Porifera and Brachiopoda; and depth to Porifera, Actinaria and Scleractinia. Other important biophysical associations were chlorophyll-*a* concentration and mixed layer depth to Actinaria; light budget to Pennatulacea; distance to the upper slope to Gorgonacea; distance to polynya to Scleractinia; bottom oxygen concentration to Brachipoda and bottom silicate concentration and salinity to Ascidiacea (Fig. 26a, Fig. 27). Most other variables were also important contributors to prediction accuracy, suggesting limited redundancy in the model.

For the biomass models, major contributors to prediction accuracy were seafloor current speed and distances to either the shelf break or upper slope (Fig. 26b). Higher seafloor current speeds were particularly important to the biomass of Porifera and Actinaria; distance to the shelf break (being the nearest area of sea floor of depth 500 m or less) to Porifera, Brachiopoda and Ascidiacea; and distance to the upper slope to Pennatulacea and Scleractinia. Also notable were the importance of sea surface temperature to Porifera; light budget to Actinaria; distance to canyon for Pennatulacea; bottom oxygen concentration and temperature to Gorgonacea; bottom nitrate concentration and temperature to Hydroida; bottom oxygen concentration to Brachiopoda; and depth to Ascidiacea (Fig. 26b, Fig. 28). Like the occurrence models, most other variables were also important predictors of vulnerable taxa biomass across East Antarctica.

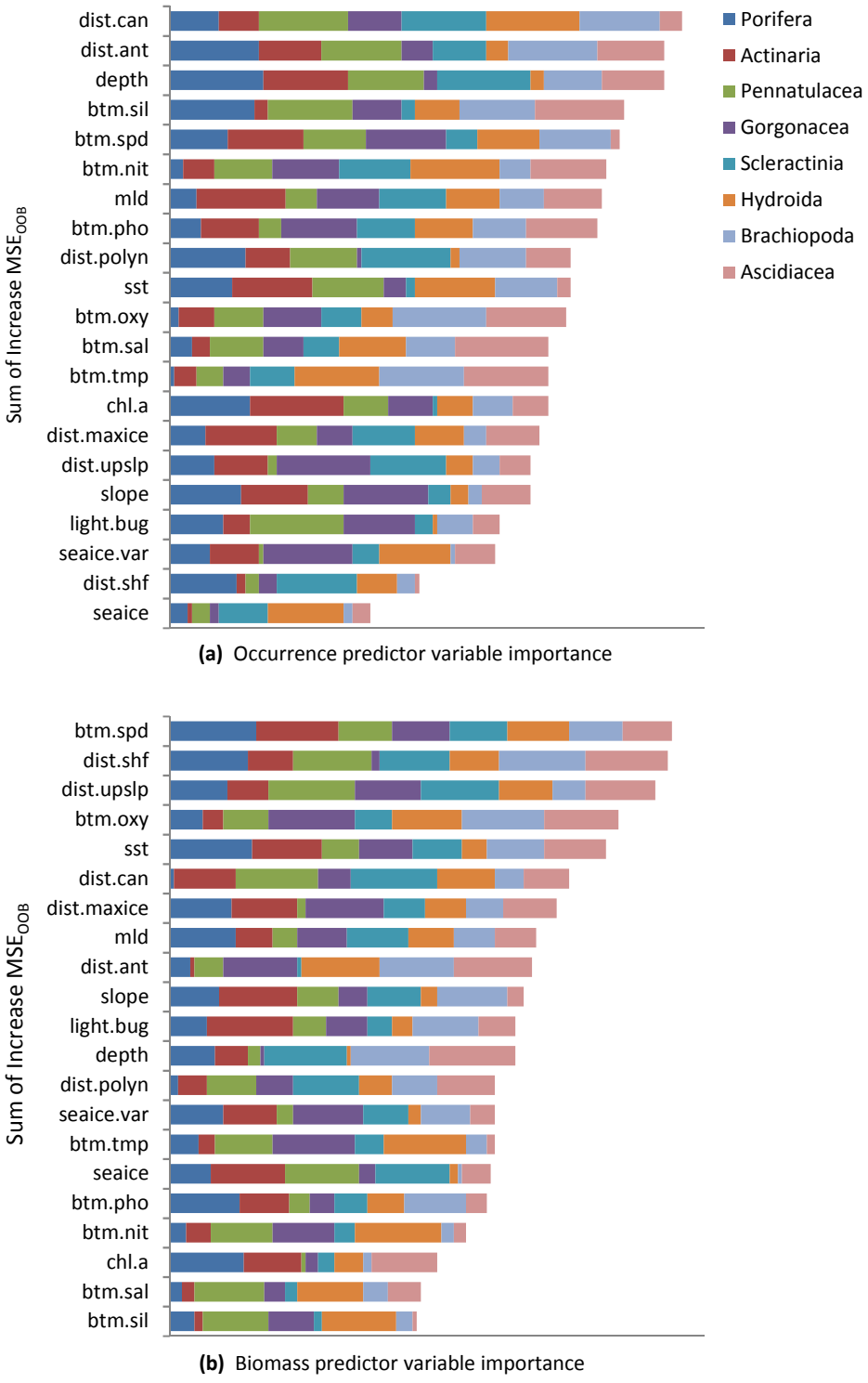

Fig. 26 Ranked accuracy importance measure (increase of MSE_{OOB}) for **(a)** occurrence and **(b)** biomass models. Increase of MSE_{OOB} values for each model/vulnerable taxa combination were ranked between 1 and 21 (the number of predictor variables) and plotted above. Predictor variable abbreviations are as in Table 18. Larger histogram bars indicated a higher importance of that variable to prediction accuracy for all taxa. For example, dist.can (distance to canyon axis) was the most important predictor variable overall for occurrence of all taxa whilst btm.spd (current speed at the seafloor) was most important to biomass of all taxa.

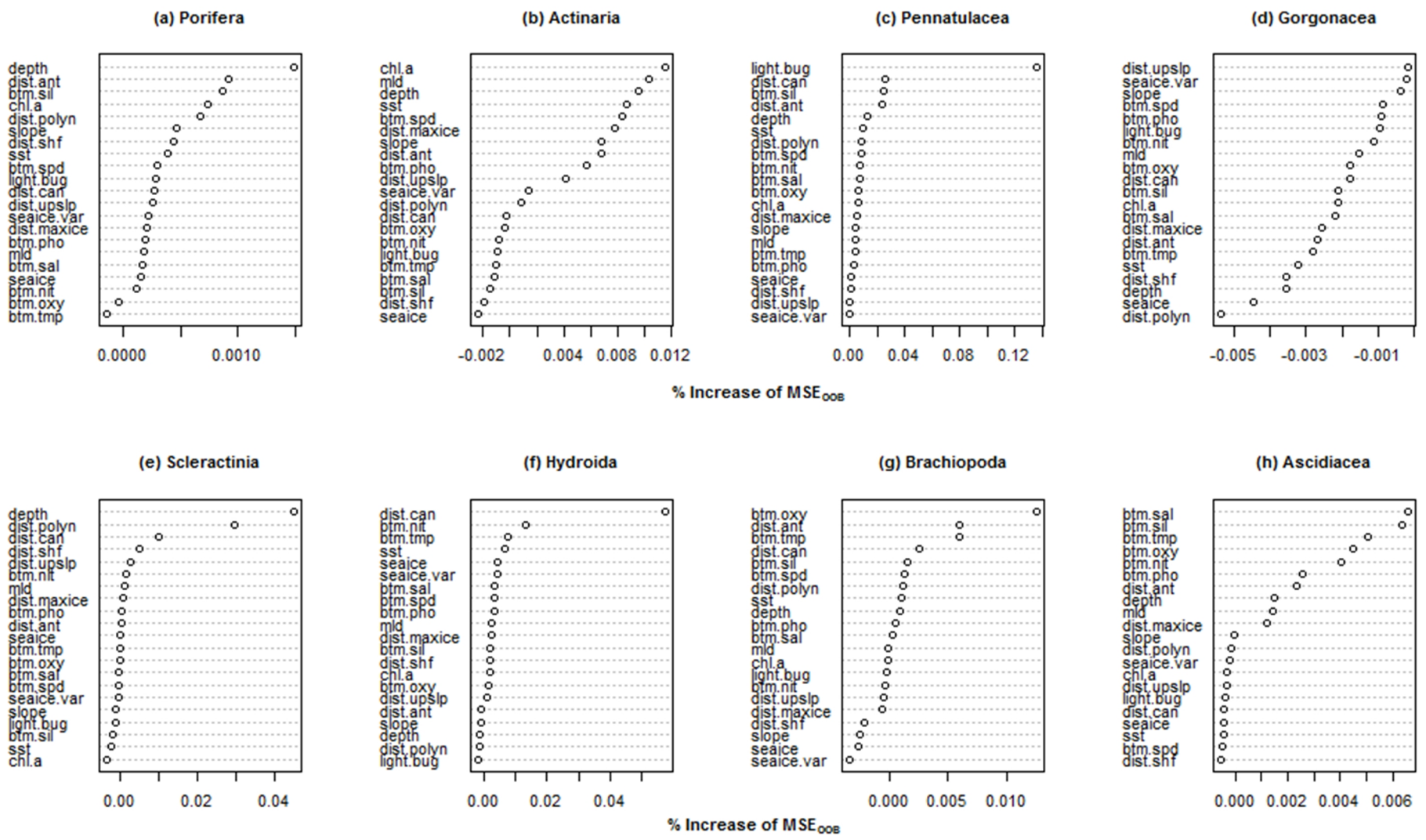

Fig. 27 Predictor importance on occurrence of vulnerable taxa across East Antarctica. Percent increase of mean square error (MSE_{OOB}) indicates the contribution to RF prediction accuracy for that variable. For example, depth was most important to Porifera occurrence in Fig. 5**a**, whilst chl.a was most important to Actinaria in Fig. 5**b**. Predictor variable abbreviations are as in Table 18.

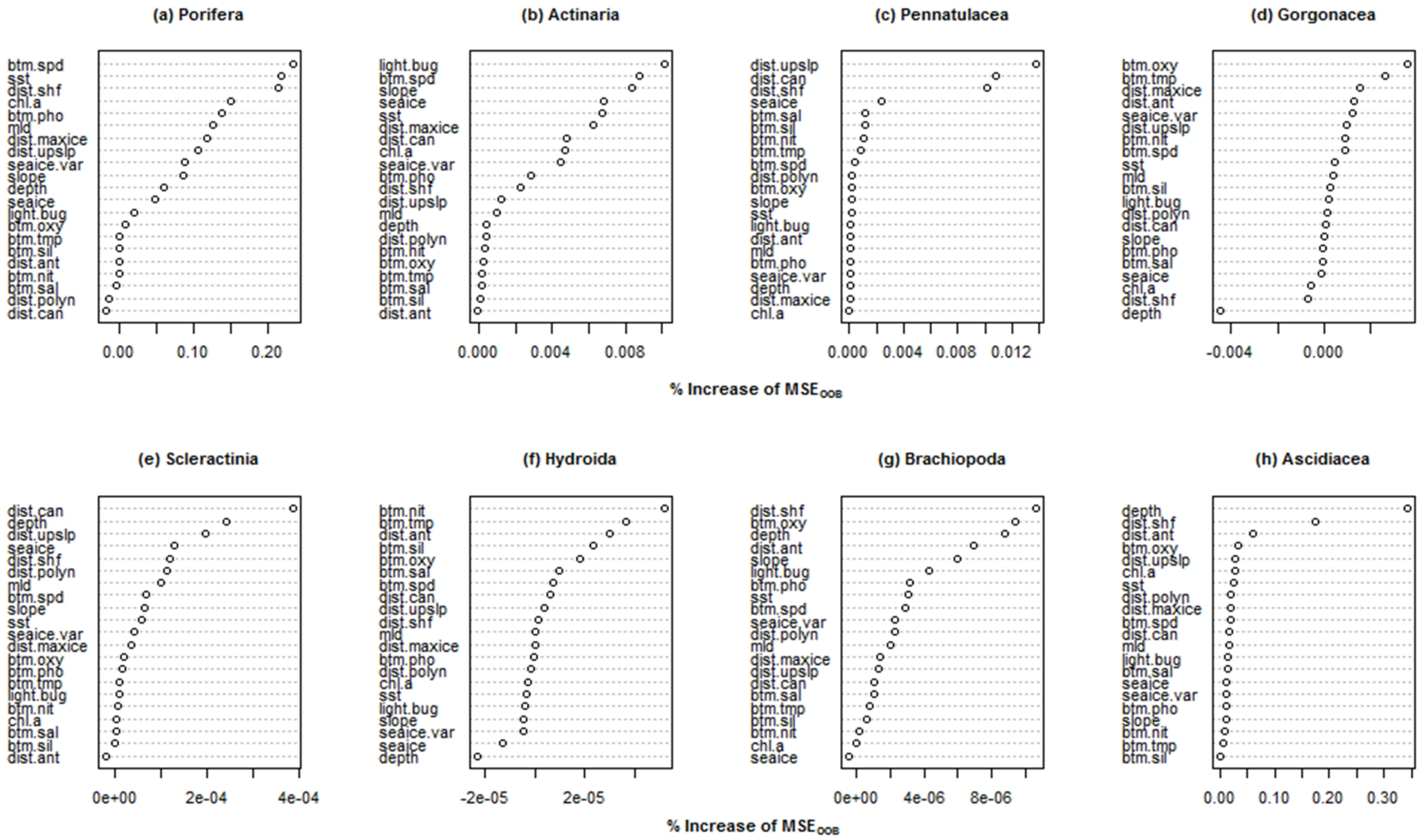

Fig. 28 Predictor importance on biomass of vulnerable taxa across East Antarctica. Percent increase of mean square error (MSE_{OOB}) indicates the contribution to RF prediction accuracy for that variable. For example, btm.spd was most important to Porifera occurrence in Fig. 28**a**, whilst light.bud was most important to Actinaria in Fig. 28**b**. Predictor variable abbreviations are as in Table 18.

4.4.3 Patterns of predicted occurrence and biomass

The spatial distribution and biomass of vulnerable taxa across East Antarctica was highly variable on a grid-cell-by-grid-cell basis (Fig. 29, Fig. 30). A high probability of occurrence did not always coincide with a high biomass. For instance, the probability of Poriferans occurring at depths shallower than ~1000 m was high (>80%) across most of East Antarctica and yet estimates of biomass were highly variable (i.e. patchy). Higher values and hotspots of vulnerable taxa were generally associated with shallow seascapes, namely Prydz Bay. Broadly speaking, other important areas included Gunnerus Ridge; much of the coast between Mawson and Mirny Stations; the area west of Casey Station; and a large area of continental shelf east between Adelie Land and George V Land. The predictions of biomass were however lower than the empirical maximums observed for most taxa (see Table 17), and hence predicted values may be considered a minimum estimate. For instance, maximum estimated biomass for Actinarians was 0.924 $g.m^{-2}$, whereas biomasses as high as 1.813 $g.m^{-2}$ were observed. This discrepancy is probably associated with the small number of trawls and unexplained variability in the model.

4.4.4 Priority areas for conservation of vulnerable taxa

The areas identified as highest conservation priority for vulnerable taxa, from 30°E to 150°E, are identified in Fig. 31. These hotspots from west to east exist on Gunnerus Ridge, west of Enderby Land, the Prydz Bay region, including waters between Mac Robertson Land and the West Ice Shelf, west of Casey Station and isolated patches between Adelie Land and George V Land. Importantly, all of these areas, aside from the area west of Casey Station, are encompassed within the proposed RSMPA.

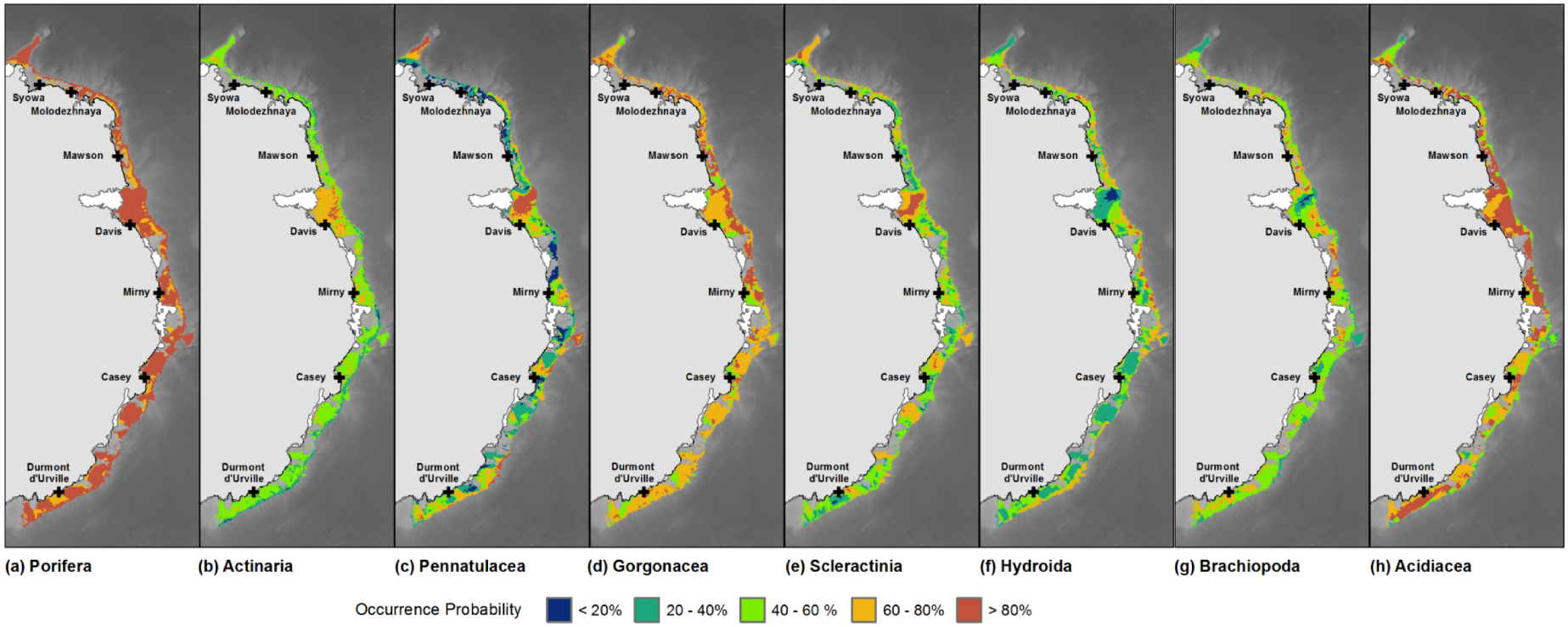

Fig. 29 Predicted occurrence of vulnerable taxa across East Antarctica between 150 m and 1500 m depth. An occurrence probability of 20%, for example, means that the probability of a vulnerable taxa occurring within the respective 0.1-degree grid cell is 20%. Grey scale is GEBCO depth.

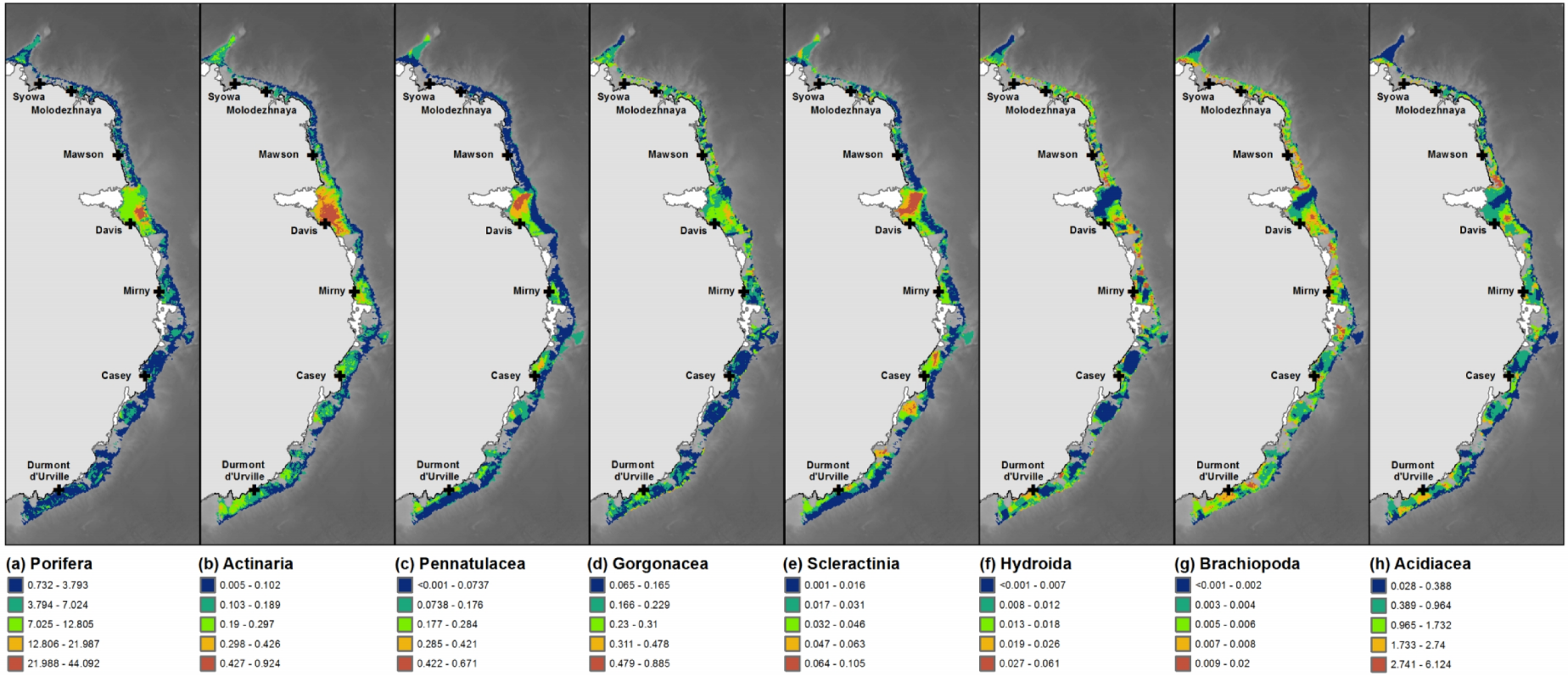

Fig. 30 Predicted biomass (g.m^{-2}) of vulnerable taxa across East Antarctica between 150 m and 1500 m depth. Grey scale is GEBCO depth.

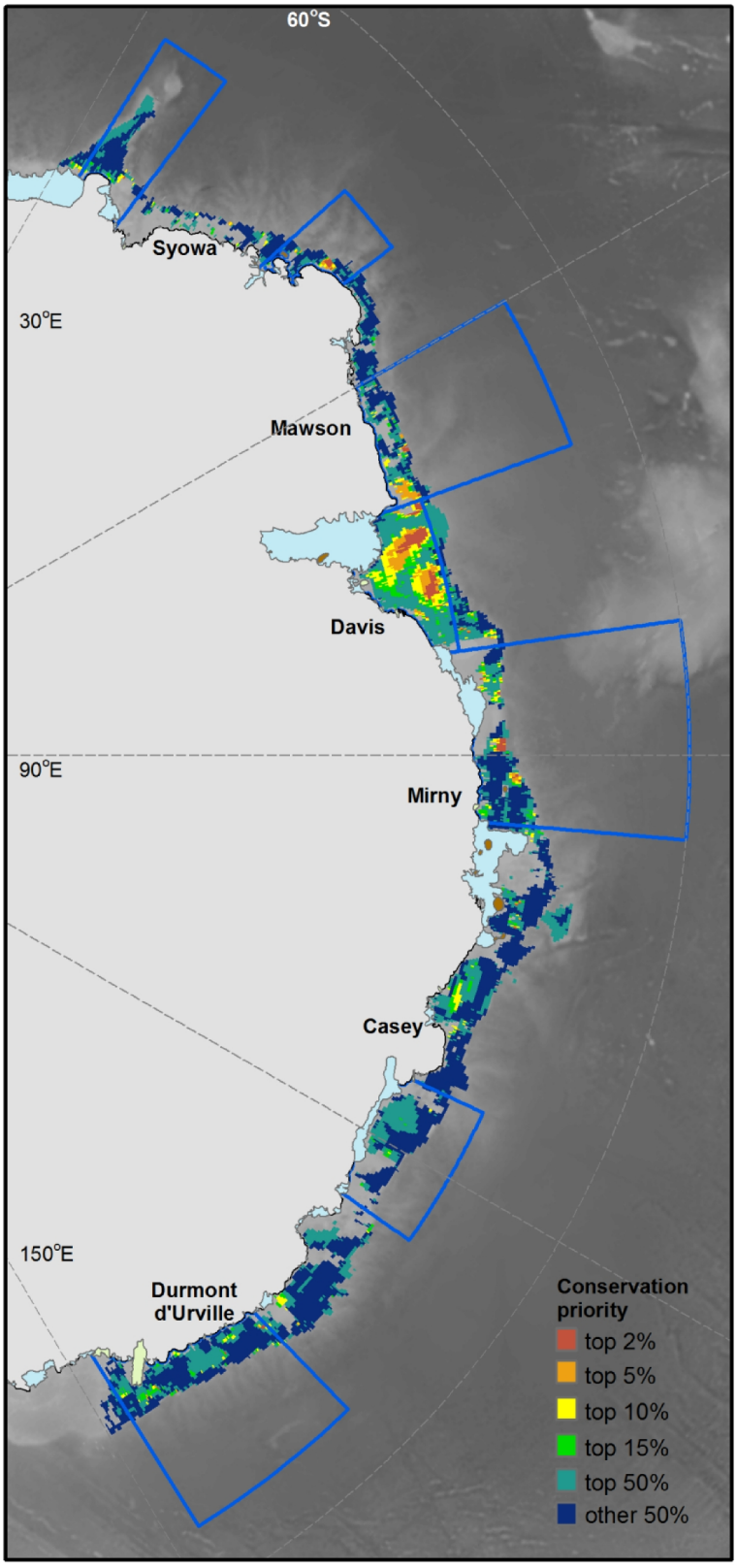

Fig. 31 Priority area for conservation of vulnerable taxa across East Antarctica between 150 m to 1500 m depth identified using Zonation. The colour of shading reflects the priority for conservation (in % of total study area); red being the areas of greatest conservation significance. Blue boxes indicate the proposed RSMPA.

4.5 Discussion

Model estimates have revealed a number of priority areas for conservation of vulnerable taxa across East Antarctica. Most of these areas, some which may be indicative of VMEs (vulnerable marine taxa), are encompassed within the RSMPA proposed by Australia, France and the European Union (AAD 2013) offering protection for these assemblages should the proposal be adopted by CCAMLR, under its mandate. The small number of empirical records, and large extent and resolution of environmental layers are potential sources of uncertainty in the model estimates. However, given the difficulties of collecting empirical data from the deep Antarctic, this study provides the synoptic assessment of benthos necessary to assist with managing biodiversity in the region, and a flexible framework for updates as new data becomes available.

4.5.1 Patterns of and proxies for vulnerable taxa

Patterns of vulnerable taxa were best described by their proximity to the nearest submarine canyon and changes in seafloor current speed. Canyons that cut the shelf break, like those across East Antarctica, are characterised by strong tidal and gravity currents which distribute phytoplankton and other detritus produced in productive coastal waters into the canyon system (Vetter & Dayton 1999). These currents also cause increased turbulence near the seafloor which resuspends particles and slows deposition, creating relatively high particulate and nutrient content in the water column (Bosley *et al.* 2004), and a greater availability of hard substrates (Hecker *et al.* 1983). Canyons are therefore associated with an enhanced food supply and availability of settlement surfaces able to sustain high densities of both motile and sessile suspension-feeders (De Leo *et al.* 2010, Vetter *et al.* 2010, Post *et al.* 2011). The occurrence of vulnerable, sessile suspension-feeders like sponges and corals in or near canyon features across the east Antarctic shelf is likely to be associated with such physical conditions.

Seafloor currents, which influence the delivery of suspended food to filter feeders, are strongly influenced by the location and orientation of the different frontal systems in the region. Three major gyres influence the Antarctic; the Weddell Sea, Prydz Bay and Ross Sea Gyres (Fig. 32). The Prydz Bay Gyres coincide with the area identified in this study as having a high occurrence probability and biomass of vulnerable taxa, and correspondingly high conservation priority. This area is also characterized by consistently high productivity (i.e. Chlorophyll-*a*) (Constable *et al.* 2010). The gyre and associated physical conditions are considered to be a strong structuring feature on the pelagic ecosystem in Prydz Bay (Hosie 1994a, b) and the results of this study suggest they are also important for the benthos. Similarly, the western edge of the Weddell Sea Gyre and eastern edge of the Ross

Sea Gyre may influence the Gunnerus Ridge and George V Land benthic assemblages respectively, as suggested by the high conservation priority of the assemblages of vulnerable taxa estimated in these regions. Other consistent hotspots of productivity include areas along the Mawson Coast, west of Casey, around Drygalski Island to the west of the Shackleton Ice Shelf and east of Durmont D'Urville (Constable *et al.* 2010); all of which were associated with hotspots of vulnerable taxa and considered high conservation priority.

Importantly, all of the regions mentioned above, except the area west of Casey, are encompassed within the proposed RSMPA suggesting the proposed management plans would be likely to achieve a high level of representativeness of vulnerable taxa across East Antarctica if adopted. This assessment is also likely to produce conservative estimates of conservation priority as predictions of biomass were lower than the empirical maximums observed for most taxa, meaning that predicted 'hotspots' of vulnerable taxa may be considered a minimum estimate. In addition this assessment ignores factors such as processes which create endemism at small spatial scales, which are known to occur in Antarctic invertebrates (Gray 2001, Clarke & Johnstone 2003) and contribute to their conservation-value.

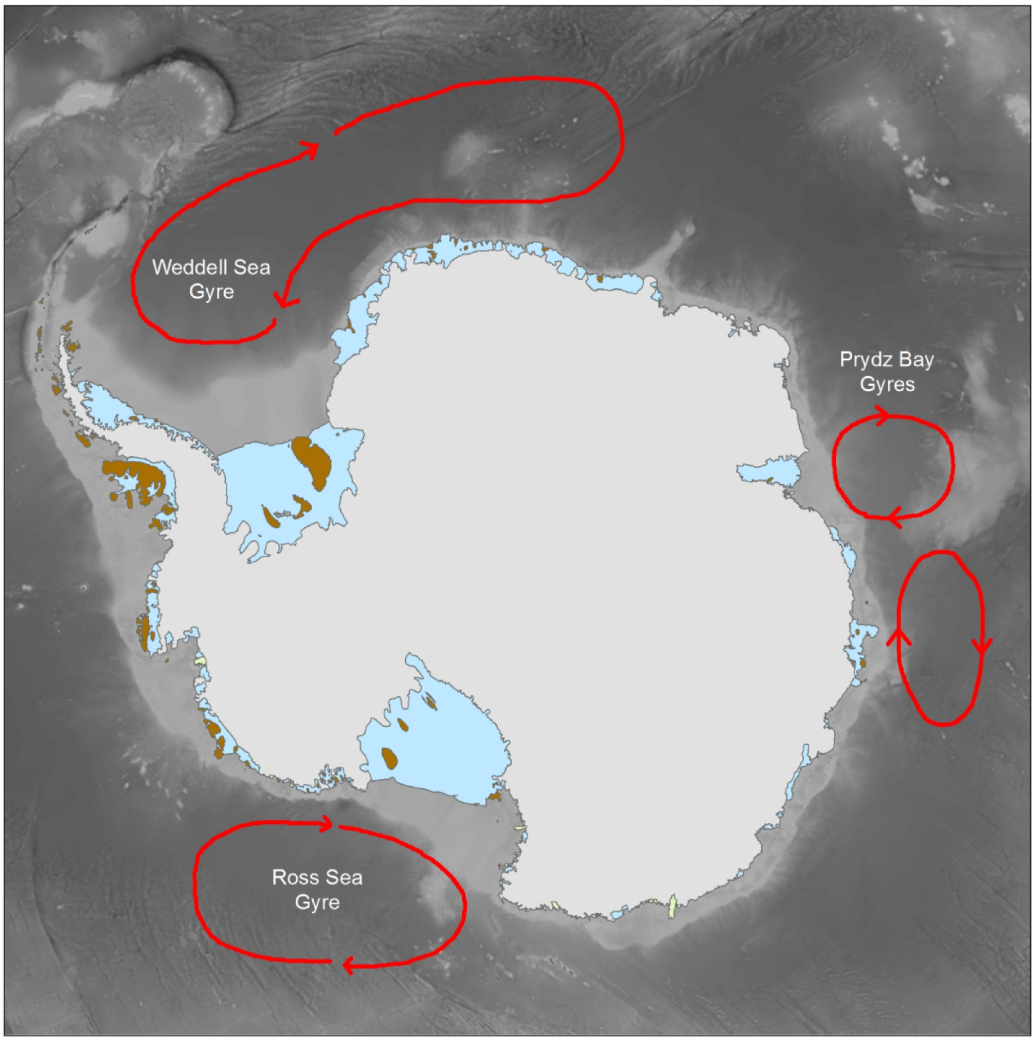

Fig. 32 Major gyres around the Antarctic continent.

4.5.2 Data and model accuracy

Both the occurrence and biomass models returned high accuracy according to the indices used, suggesting a high level of confidence in these predictions at the applied fine spatial scale (0.1-degree). However, potential sources of uncertainty should be considered when interpreting these predictions.

First, the analyses were based on only 34 trawl samples taken from within a relatively small sub-set of the area of interest and with frequent non-detections for some vulnerable taxa. Hence predictions and resulting inferences of 'biodiversity hotspots' may be influenced by the spatial heterogeneity of the empirical data, resulting in favoured distributions of vulnerable taxa (i.e. favoured to sampled areas). Meynard and Quinn (2007) examined the performance of a suite of models under such circumstances, concluding that classification trees (like RF) tended to have good predictions of

species presence, but poor predictions of species absences, when sample size was small (<150 samples) and species were infrequent (<5% of samples) (Meynard & Quinn 2007). In this study the occurrence models provided an excellent discrimination between areas of presence or absence. However the biomass models did exhibit a tendency to over-estimate values in instance of zero observations (i.e. species absent) and hence model accuracy would likely benefit from additional empirical data. This suggests that patchiness in the benthic habitat and discontinuities between patches were underestimated, which may lead to underestimates of conservation priority in *Zonation* and the distribution of hotspots of vulnerable taxa (e.g. inside versus outside the RSMPA). A combined approach of modelling presence, absence and abundance might be explored to evaluate these uncertainties and potential biases.

Models were conducted at a coarse taxonomic level, e.g. Order, which means assumptions have been made that all species within the order respond to the same defined set of environmental conditions, which is undoubtedly an oversimplification. The order Gorgonacea, as an example, includes more than 500 different species globally (UDEL 2007), suggesting a wide range of physical tolerances for species within this group. In Antarctica, many species are endemic to the region, and adapted to similarly cold, stable environmental conditions common to the deep Southern Ocean (Gray 2001, Clarke & Johnstone 2003). It is therefore reasonable to assume that species within broad taxonomic groups, like Gorgonacea, may respond similarly to environmental gradients. Nevertheless, some species within these groups may have different environmental dependencies, introducing a potential source of bias in the model. Similarly factors such as competition, predation and dispersal of larvae will affect the distribution of biota but were not explicitly considered in this study.

The temporal and spatial resolution of the underlying biological data is also a possible source of uncertainty. Firstly, benthic data were collated from two surveys conducted 10 years apart and hence the seascape and its benthos may have changed over this time period. However the slow growth, maturation and great longevity of many Antarctic benthos (Arntz *et al.* 1997), and the relatively stable environments in which they reside, would suggest limited change over this duration. The most likely reason benthos might have changed in the last 10 years would be fishing. However the lack of wholesale bottom fishing activity in the east Antarctic (CCAMLR 2013), and conservation measures preventing fishing in waters shallower that 550 m, would suggest minimal temporal change between the two surveys. For example at HIMI, there didn't appear to be a detectable effect of fishing on habitats sampled over multiple years despite considerable fishing effort for more than a decade (Chapter 2). Secondly, the gridded values which are input into this analysis contain values which have been interpolated from the original data points which can introduce uncertainty (Post 2006).

Plus, further uncertainty is introduced through extrapolation across larger physical gradients than those tested (e.g. deeper than sampled during AA97 or AA09) (Post 2006). In addition, the clumped distribution of samples means that spatial autocorrelation may be encountered, and if not properly addressed, may influence the statistical inference of the models (Lichstein *et al.* 2002, Dormann 2007, Dormann *et al.* 2007). I explored whether there was spatial autocorrelation in the data for each vulnerable taxa by calculating Moran's *I* (Moran 1950) and Geary's *C* (Geary 1954) and in doing so found little evidence for spatial autocorrelation in either the occurrence or the biomass of vulnerable taxa (Table 19). Lastly, the beam trawl won't necessarily have collected every taxa. Hence estimates may be biased toward more readily sampled taxa (e.g. large sponges), and underestimate those more difficult to sample biota (e.g. encrusting bryozoans). A combination of biological samples for composition, and video footage for representativeness (i.e. did sampling collect everything observed), would assist in providing a more comprehensive estimate of biodiversity.

Table 19 Spatial autocorrelation in data for each vulnerable taxa assessed using Moran's I and Geary's C. Moran's I ranges from -1 (perfect dispersion) to +1 (perfect correlation), with values around zero indicative of a random spatial pattern. Geary's C ranges from 0 to 2, with values around 1 indicative of a random spatial pattern.

	Moran *I*		**Geary's *C***	
Taxa	Occurrence	Biomass	Occurrence	Biomass
Porifera	-0.0277	-0.0243	0.9576	0.9912
Actinaria	-0.0257	-0.0277	0.9951	1.0017
Pennatulacea	-0.0485	-0.0332	1.0176	1.0102
Alcyonacea	-0.0342	-0.0324	0.9976	1.0066
Scleractinia	-0.0336	-0.0325	1.0028	1.0076
Hydroida	-0.0336	-0.0339	1.0028	1.01
Brachiopoda	-0.0313	-0.0262	1.0014	0.9993
Ascidiacea	-0.0267	-0.0131	0.9933	0.9655

4.5.3 Further research

The models developed here can readily incorporate new data, and the use of a standard set of diagnostics allows the evaluation of the effect of including new data on modelling sensitivity. Additional benthic data are available for East Antarctica, but were not included in this study due to differences in the gear-type used and the type of data collected (i.e. presence-only). Further studies might enable the combination of these different data types (e.g. Fithian *et al.* 2015) and their use to further train the model, or as a means of external validation. Similarly, new or higher resolution layers of environmental variables are continually being produced which could also be included to increase model accuracy. For instance, substrate-type is often considered as a proxy of benthic biodiversity (McArthur *et al.* 2010) and if available/included in this study, would most likely increase the variance explained in the model. In addition, I used annual means for remote sensing

data, but there is potential that finer temporal data, i.e. quarterly or biannual, could be used in the future to further refine predictions

4.6 Conclusions

While the impacts of bottom fishing on Antarctic benthic communities are still poorly understood, inference from studies in other parts of the world suggests that fishing has the potential to alter benthic ecosystems. As natural disturbance below 500 m depth appears to be infrequent, it has been suggested that bottom fishing may be the major disturbance agent in the Antarctic in fishable depths (550-2000 m) (CCAMLR 2009a).

In the face of the substantial uncertainty associated with the impacts of bottom fishing disturbance outlined above and the recognized necessity for precautionary management in the Southern Ocean (CCAMLR 2008), the most straightforward and risk-averse strategy is to maintain substantial areas that are closed to fishing. To designate these areas requires an understanding of the benthos, which I show can be ascertained with some confidence from available data and models. Given the immediacy of the issue of managing bottom fishing to prevent significant adverse interactions with vulnerable habitats and the mandate for the establishment of a RSMPA globally, the estimates presented here support the proposed RSMPA as achieving representative protection of VME taxa in this region. However, potential biases owing to the heterogeneity and small sample size of the empirical data must to be considered in the decision-making process; uncertainties that would best be addressed by target benthic sampling across the East Antarctica.

Discussion

Characterising HIMI benthic communities and the effects of bottom fishing on a sub-Antarctic ecosystem

The extensive sampling of HIMI has revealed a typical high latitude benthic fauna dominated by slow growing, sessile suspension-feeders and echinoderms, including many taxa common to the Southern Ocean. This indicated strong faunal affinities between HIMI, the Antarctic and other sub-Antarctic seascapes. However, intermediate-scale richness and diversity relative to, for example, continental Antarctica (Gutt & Starmans 1998) or Australia (Williams *et al.* 2010), in combination with high numbers of undescribed and locally rare taxa (i.e. restricted to one station), infer a degree of isolation and uniqueness in the HIMI benthos. Hence, like Bouvet Island (Gutt *et al.* 2006), 'restricted isolation' may be the most appropriate way to consider the biogeographic context of benthic fauna at HIMI. A general conclusion about the relative diversity of benthos at HIMI compared with communities elsewhere was however, hampered by variation in sampling methodology (e.g. gear type), sample representativeness (i.e. did sampling capture all biodiversity) and taxonomy (e.g. unclassified groups), meaning that biodiversity estimates were conservative. Nonetheless, the level of sampling undertaken for this study was shown to be effective at representing the local diversity at HIMI, at least in regard to the more abundant megabenthos, which were the focus of this assessment.

The dominance of sessile fauna and levels of endemism in some groups highlight the particular vulnerability of benthic communities and reiterate the importance of conservation measures to be implemented at HIMI. Long-lived, slow-growing, habitat-forming taxa such as corals and sponges that characterise the HIMI benthos are known to be particularly vulnerable to impacts by bottom fishing gears (e.g. Collie et al. 1997, Koslow et al. 2001). Similarly, rare or endemic taxa, which are often range-restricted due to a low fecundity and dispersal potential, are likely to have a poor ability to recover following damage or mortality leading to population decline. Industrial fisheries using bottom fishing gear have occurred in the Southern Ocean since the 1960s and at HIMI specifically since 1997, raising concerns over potential impacts. However, disturbance from bottom fishing was not identified as an important proxy for the distribution and abundance of benthos despite extensive trawling in the area. Instead patterns of biota were best explained by environment factors including seafloor current speed and POC concentration, which may well mask any impacts owing to bottom fishing. This result was surprising considering that others have shown such strong links between diversity, abundance and community structure in fished and un-fished habitats (e.g. Collie et al. 1997, Koslow et al. 2001), but does highlight the importance of stable environmental conditions to patterns

of biodiversity and population maintenance. It should be noted, however, that my study could not sample some of the most heavily trawled areas at HIMI and hence further sampling across a greater disturbance range might alter these conclusions.

Application of predictive modelling to marine planning and management

Patterns and predictors of benthic biodiversity were broadly similar to those observed in other studies in relation to depth, food availability and geomorphic features (e.g. Branch *et al.* 1993, Jennings *et al.* 1999b, Starmans *et al.* 1999, Ward *et al.* 2006b, Wei *et al.* 2010). The distribution and abundance of most vulnerable taxa decreased with increasing depth and decreasing food supply (i.e. concentration POC or Chlorophyll-*a*); and both are widely recognised associations between physical variables and megabenthos (Denisenko *et al.* 2003, Jones *et al.* 2007, Smale 2008, Wei *et al.* 2010). Canyons and banks/seamounts were identified as particularly important habitats for the benthos. The productive, turbulent conditions characteristic of these features have been shown to sustain enhanced diversity and a high biomass of benthos compared with surrounding shelf or plateau habitats (Koslow & Gowlett-Holmes 1998, Vetter & Dayton 1999, De Leo *et al.* 2010, Vetter *et al.* 2010). In contrast, the deep waters of HIMI and East Antarctica were characterised by low diversity and biomass, at least in regard to the megabenthos. This suggests that MPAs which protect shallower depths, complex geomorphic features (e.g. canyons) and areas of high productivity will be better situated to achieving CAR principles for the benthic habitats, at least in regard to hotspots of sessile suspension-feeders. The deeper areas across both seascapes were less well sampled (>500 m depth), however were seen to support lower biomasses overall, and hence were attributed a lower conservation priority value. This does not, however, preclude the existence of locations where important aggregations of benthos are present but were not sampled and, therefore, were unable to be identified in this study.

Using the HIMI dataset and physical surrogates I successfully developed a framework to model and predict the spatial distribution and abundance of vulnerable taxa, and to identify priority areas for conservation across seascapes. RF was deemed the better method out of four models trialled due to good accuracy, high calibration and low bias for both the occurrence and biomass datasets, and hence predictions of vulnerable taxa were made and scrutinised using this approach. Analyses of these predictions in *Zonation* highlighted HIMIs banks and numerous areas across the central plateau and continental slope as priority areas for conservation, most of which were above 500 m depth, and currently protected by the MPA. Unique characteristics of Pike Bank and predicted hotspots of vulnerable taxa outside the MPA (i.e. on the central plateau and south of Shell Bank) may warrant special conservation measures or consideration for inclusion within the existing MPA. Nonetheless,

it was identified that 29% of the highest conservation priority areas for vulnerable taxa are encompassed within the HIMI MPA, which exceeds the conservation target of 10% (Target 11) set by the Convention on Biological Diversity in 2010, and almost meets the target of 30% set by the International Union for the Conservation of Nature in November 2014. This suggests that the Australian government is well positioned to meet conservation targets in regard to vulnerable marine benthos and the HIMI MPA. Similarly, model estimates for East Antarctica revealed a number of hotspots, almost all of which were encompassed by the RSMPA proposed by Australia, France and the European Union (AAD 2013), offering protection for these assemblages should the proposal be adopted by CCAMLR.

Uncertainties and implications for decision makers

The occurrence and biomass models for Antarctic and sub-Antarctic communities returned high accuracy according to the indices used, suggesting a high level of confidence in the predictions at the applied spatial scale, and highlighting the transferability of the RF framework to other seascapes. However, potential sources of uncertainty should be considered when interpreting these predictions.

First is the quantity of available biological data, which was particularly limited for East Antarctica. Numerous authors have shown that sample size and the number of presence records greatly influences model performance and, not surprisingly, suggest that model accuracy would benefit from further targeted sampling (McPherson *et al.* 2004, Reese *et al.* 2005, Guisan *et al.* 2006a, Meynard & Quinn 2007). In this study the occurrence models provided an excellent discrimination between areas of presence or absence. However the biomass models did have a tendency to over-estimate values where there were zero observations (i.e. species absent) and hence model accuracy would likely benefit from additional empirical data. This also indicates that patchiness in the benthic habitat and discontinuities between patches were underestimated, which may lead to underestimates of conservation priority. A combined approach of modelling presence, absence and biomass could be useful.

The second source of uncertainty is the underlying environmental data used as surrogates for biodiversity. Many of the variables used here and in similar studies (e.g. Wei *et al.* 2010) are derived from the sea surface (e.g. remote sensing estimates of SST or Chlorophyll-*a* concentration) and yet the relationship between these easily measured proxies and conditions at the seafloor that actually promote aggregations of benthos are poorly known. Hence there is a possibility that the relationships observed may be coincidental. Plus, further uncertainty is introduced through extrapolation across larger physical gradients than those tested (e.g. deeper than sampled) (Post 2006).

Temporal variability in the benthic fauna and assemblages is another potential source of model uncertainty. Benthic data for HIMI and East Antarctic seascapes were collected over a series of years and hence the seascape and its benthos may have changed over this time period and confounded spatial predictions. The slow growth, maturation and longevity of many Southern Ocean benthos (Arntz et al. 1997), and the relatively stable environments in which they reside, would suggest limited temporal change will have occurred among surveys spanning 10 years. The most likely reason benthos might have changed across such a short time span would be anthropogenic effects such as fishing. However at HIMI there didn't appear to be a detectable effect of fishing on habitats despite considerable fishing effort for more than a decade. In East Antarctica, bottom fishing is exploratory, limited in extent, and excluded in waters shallower that 550 m (CCAMLR 2013), suggesting that temporal variability owing to fishing was unlikely.

Models were constructed at a coarse taxonomic level, e.g. Order, which means assumptions have been made that all species within an Order respond to the same defined set of environmental conditions, which is undoubtedly an oversimplification. The order Gorgonacea, as an example, includes more than 500 different species globally (UDEL 2007), suggesting a wide range of physical tolerances for species within this group. In Antarctica and the sub-Antarctic, many species are endemic, and adapted to similarly cold, stable environmental conditions common to the deep Southern Ocean (Gray 2001, Clarke & Johnstone 2003). It is therefore reasonable to assume that species within broad taxonomic groups, like Gorgonacea, may respond similarly to environmental gradients. Nevertheless, some species within these groups may have different environmental dependencies, introducing a potential source of bias in the model. Similarly factors such as competition, predation and dispersal of larvae will affect the distribution of biota but were not explicitly considered in this study.

Finally, the choice of modelling approach may affect the results as predictions often vary between methods (Meynard & Quinn 2007). A comparison of GLM, GAM, BRT and RF identified RF as the "best" method to analyse the HIMI dataset, but there are other modeling approaches (such as mixed models) that were not considered here due to sample size and research constraints. Thus, application of other methods may result in different predictions.

Conclusions and future directions

The model estimates presented in this study suggest that CAR (comprehensive, adequate and representative) principles have been achieved for vulnerable benthos in the HIMI and (proposed) East Antarctic MPAs. In developing these MPAs, the distribution and hence representativeness of

protection for benthic habitats and their biota within the MPA was inferred largely from physical variables (Constable *et al.* 2010, Welsford *et al.* 2013). This was necessary as empirical data required to characterise these habitats were sparse or not available at the time (Constable *et al.* 2010), and still are for East Antarctica. My predictive modeling results that do incorporate empirical data and have produced similar recommendations for biodiversity conservation at HIMI and in East Antarctica suggest that the use of physical surrogates are an adequate tool for marine planning in the absence of biological data in these systems. More broadly, the results suggest that management or mitigation measures for benthos based on physical parameters may provide adequate precautionary management in other marine ecosystems where the empirical data necessary to evaluate the benthic habitat are lacking.

The accuracy of predictions and transferability of the RF framework means that methods developed here might be readily applied to other seascapes where decision making may benefit from predictions. There are uncertainties which must be considered when applying predictions in marine conservation planning decisions. For HIMI and East Antarctica these uncertainties are born through sample size, model extent and data resolution - all potential issues for modelling of deep-sea ecosystems. Collating additional data and incorporating it into the model would assist with addressing these uncertainties. For instance, additional benthic data are available for HIMI and East Antarctica but these were not included in this study due to differences in the gear-type used and the type of data collected (i.e. presence-only). Further studies to address ways of combining different data types into a similar modeling framework may increase the accuracy and utility of predictions without large investments in benthic surveys and additional data collection (e.g. Fithian *et al.* 2015). Similarly, new or higher resolution layers of environmental variables are continually being produced which could also be included to increase model accuracy (e.g. substrate-type). In addition, biotic factors such as competition and predation will affect the distribution of biota, and incorporating such factors into the model may also further improve accuracy and add realism to predictions (e.g. abundance of toothfish at HIMI). The models developed can readily incorporate new data, and evaluate the effect of including those new data on modelling sensitivity, meaning that predictions can be readily refined and improved. Nonetheless, further model parameterisation does not denote the need for empirical sampling to test the models' predictions. Particularly so for those the high conservation-value areas identified by the models that fall outside the HIMI MPA and the Antarctic RSMPA, i.e. Pike Bank in the HIMI region and the area west of Casey off East Antarctica.

This study has contributed to addressing a significant gap in our understanding of deep-sea benthic ecosystems in areas where bottom fisheries are a concern, particularly for corals, sponges and other

habitat-forming taxa, and has demonstrated the utility of predictive modelling to inform marine spatial planning and management. Given the immediacy of the issue of managing bottom fishing to prevent significant adverse interactions with vulnerable ecosystems, and the practical difficulties associated with obtaining empirical data, surrogate-based predictions like those presented in this study provide the only practical means to make reasoned decisions about high seas resource management and for the establishment of a CAR system of MPAs throughout the Southern Ocean.

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